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Effects of human disturbance on vocalizations of the Sumatran Orangutan in North Sumatra, Indonesia: conservation implications

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Orang-utan

“Person of the forest”

Bahasa Indonesia

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Resumo

A expansão humana ameaça não só toda a biodiversidade mas também os serviços que esta fornece e dos quais dependemos. Actividades como a desflorestação, a conversão agrícola, a caça ilegal e o tráfico de animais potenciam o desaparecimento dos ecossistemas e a extinção de espécies a estes associadas, com graves consequências também para o ser humano. A desflorestação foi responsável pela destruição de 230 milhões de hectares de floresta somente entre o período de 2000 a 2012, sendo que as florestas tropicais são dos biomas mais afectados por tal perturbação. A desflorestação é frequentemente acompanhada pela conversão de solo para fins agrícolas, o que acaba por fragmentar as paisagens, alterar a sua conectividade e criar novos acessos a zonas até aí livres da intervenção humana. Esta fragmentação não só aumenta o número de conflitos entre a fauna selvagem e o ser humano, dado o maior contacto entre ambos, como também potencia a caça e a captura de animais vivos para mercados ilegais ou a venda directa.

Os grandes símios, um dos grupos animais sob os quais a pressão humana mais se faz sentir – sendo também o grupo ao qual pertencemos, em conjunto com o Gorila *Gorilla spp*., o Chimpanzé *Pan troglodytes*, o Bonobo *Pan paniscus* e o Orangotango *Pongo spp*. – vêem-se ameaçados devido aos seus longos ciclos reprodutores e exigentes necessidades ecológicas, sendo, por isso, extremamente vulneráveis à desflorestação, à fragmentação das paisagens e à caça e captura ilegais. Uma das regiões do globo onde estes fenómenos mais se fazem sentir é o Sudeste Asiático, onde o crescimento populacional e a desflorestação tomam proporções cada vez maiores. A adequabilidade dos terrenos para o cultivo de bens essenciais, como o óleo de palma *Elaeis guineensis*, a cana-de-açucar *Saccharum officinarum*, ou a árvore-da-borracha *Hevea brasiliensis*, e o reduzido custo de produção das mesmas, tornam esta área do globo extremamente requisitada para a apreensão de espaço e recursos. É aqui que encontramos um dos grandes símios mais ameaçados do planeta: o orangotango da Sumatra, *Pongo abelii*.

O orangotango da Sumatra, juntamente com o orangotango do Bornéu, *Pongo pygmaeus*, formam o único género de grandes símios que está presente fora do continente Africano. Tendo sido a primeira linhagem dos grandes símios a se separar das restantes, os orangotangos são os únicos grandes símios quase exclusivamente arborícolas e considerados dos menos sociais, organizando-se numa estrutura de fissão-fusão, onde os encontros são pouco comuns e geralmente breves, exceptuando momentos de acasalamento que podem durar até vários dias. Ambas as espécies de orangotangos são sexualmente dimórficas, sendo o macho consideravelmente maior, e alguns indivíduos, após atingirem a maturidade sexual, desenvolvem flanges. Estas são um caracter sexual secundário que se exprime sob a forma de discos de matéria adiposa na face, e que acompanham o início do uso das "long-calls", um chamamento característico desta faixa etária, fundamental na coesão social dos orangotangos.

Embora ambas as espécies de orangotangos sejam consideradas "Criticamente em Perigo" pela IUCN, as populações de orangotangos da Sumatra são hoje consideravelmente menores do que as da sua espécie irmã. A última avaliação do estado destas populações indicava que existiam cerca de 14613 orangotangos da Sumatra e 54000 do Bornéu. Grande parte dos orangotangos que residem na ilha da Sumatra vivem dentro e nas imediações do Parque Nacional de Gunung Leuser, que é partilhado por duas províncias, a Sumatra do Norte e Aceh. Ambas têm-se desenvolvido excepcionalmente nos últimos anos, em especial Aceh, devido ao gás natural, o que tem levado ao contínuo decréscimo não só das populações de orangotangos, mas também de outras espécies icónicas e endémicas desta ilha, como o tigre-da-Sumatra *Panthera tigris sumatrae* ou o elefante-da-Sumatra *Elephas maximus sumatranus*.

Dado o crescente conflito e competição entre o homem e a vida selvagem, seja a nível de espaço ou de recursos, torna-se cada vez mais imperativo compreender como é que as espécies respondem às perturbações causadas pelo homem, de maneira a podermos proteger as suas populações e gerir e potenciar os seus serviços. Uma das maneiras da vida selvagem reagir a tais distúrbios é através dos seus sistemas de comunicação, maneira pela qual transmitem informação seja a outros membros da mesma espécie, seja à comunidade, ou até mesmo à fonte de perturbação no sentido de a demover e afastar. Uma das vertentes mais abordadas da comunicação são as vocalizações, nomeadamente os chamamentos de alarme, que são uma peça-chave na compreensão da dinâmica de interacção entre a espécie e o seu predador, ou outro tipo de perturbação, como o da presença humana. Os chamamentos de alarme são produzidos quando uma fonte de perigo é detectada, servindo para dar o alerta aos outros membros do grupo e/ou para sinalizar à fonte de perigo que esta foi detectada.

Em orangotangos existem alguns chamamentos descritos como chamamentos de alarme, sendo os mais observados o *Kiss-Squeak* e o *Grumph*. Estes chamamentos são usados pelos orangotangos em encontros com os seus predadores naturais, sendo o mais importante o tigre-da-Sumatra, mas também em encontros com seres humanos. Quando os animais, e os orangotangos em particular, respondem com chamamentos de alarme a perturbações no seu habitat, seja pela presença de tigres, seja pela presença de seres humanos, eles estão a alocar tempo e energia a essa actividade em detrimento de outras actividades. Dado o caracter invasivo e persistente das actividades humanas no habitat natural do orangotango, o tempo e energia despendidos a vocalizar na presença de seres humanos – perturbação humana – pode reduzir significativamente o tempo útil total alocado à alimentação, reprodução, cuidados parentais, descanso e bem-estar em geral. As consequências dos distúrbios humanos podem até afectar a condição corporal e o fitness dos animais de forma semelhante à pressão exercida pelos seus predadores naturais, como sugerido na hipótese de risco-distúrbio proposta por Alejandro Frid e Lawrence Dill, em 2002. Quando assim é, a perturbação humana deve ser considerada como mais um factor a contribuir negativamente para o estatuto de conservação das espécies.

Como tal, o objectivo deste trabalho foi o de explorar esta hipótese de forma a compreender o impacto da perturbação humana numa população de orangotangos da Sumatra, focando-nos nas suas vocalizações. Esta população reside dentro do Parque Nacional de Gunung Leuser, cuja área foi alvo de programas de deflorestação há poucas décadas. Focámo-nos, essencialmente, nos chamamentos de alarme, de modo a conseguirmos medir o seu estado de alerta na presença de humanos e o esforço que este poderá representar comparativamente ao esforço empregado pelos orangotangos na presença de tigres.

A maioria dos dias (sessões de mostragem) em que os orangotangos foram seguidos por um grupo de observadores humanos (investigadores e guias) houve produção de vocalizações direccionadas para os observadores, num total de 12 chamamentos diferentes. Como esperado, a grande maioria foram efectivamente chamamentos de alarme, demonstrando que os orangotangos são sensíveis à presença humana e que a percepcionam como um distúrbio. As duas vocalizações mais utilizadas foram o "*Kiss-Squeak*" e uma variação deste chamamento, o "*Kiss-Sequeak Hand*", que torna o chamamento mais grave, criando a falsa impressão de que o orangotango que o emite é maior do que o seu tamanho real. São, no entanto, vocalizações pouco agressivas, comparativamente ao *Complex Call*, que foi só raramente produzido. Houve também algum grau de habituação à presença humana – já que o grupo de observadores era sempre o mesmo e não era agressivo. Estes dois resultados sugerem que a resposta à presença humana, apesar de ser uma resposta de alarme, é uma resposta moderada. No entanto, depois de compararmos o esforço de chamamento dos orangotangos perante os observadores humanos com o esforço destes, descrito na literatura, perante tigres – e tendo em conta a abundância de tigres na Sumatra – descobrimos que a frequência de chamamentos, a duração de chamamentos e a duração dos estados

de alarme podem ser iguais ou superiores aos utilizados com os tigres. Portanto, apesar de a resposta dos orangotangos à presença humana aparentar ser moderada, ela parece indicar que os humanos induzem comportamentos crónicos de evasão-risco, semelhantes àqueles induzidos pelos seus predadores naturais. Isto indica que, com base em vocalizações de resposta ao perigo, a hipótese de risco-distúrbio se comprova em orangotangos. Quer a frequência, quer a duração dos chamamentos e dos estados de alerta constituem uma alocação significativa de tempo, o que pode indicar que a presença humana tem bastante impacto nas actividades dos orangotangos. Ainda assim, os dados recolhidos podem não representar o dispêndio real de energia dos orangotangos, pois não tivemos em conta o tempo de recuperação de um orangotango após um encontro com o ser humano.

Este é o primeiro trabalho a testar a hipótese de risco-distúrbio em orangotangos e em grandes símios, em geral, demonstrando pela primeira vez que as actividades humanas podem também ter este tipo de impacto nestas espécies emblemáticas. O contacto prolongado com o ser humano devido à diminuição e constrição do habitat pode, assim, ter mais esta repercussão negativa para os animais, para além de todas as que já contribuem, directa – caça p.e. – e indirectamente – desflorestação e conversão de solo p.e. – para a diminuição das suas populações.

Palavras-chave: Orangotango, vocalizações, hipótese risco-distúrbio, perturbação humana, conservação

Abstract

Forest loss, land conversion, poaching and illegal trading are some of the major drivers for the loss of biodiversity and ecosystem services. As conflict between humans and wildlife increases, comprehending how wildlife responds to human disturbances in the wild becomes vital to the sustainability of species, ecosystems and ultimately human kind. Vocalizations are a key feature to understand the interaction dynamics of a species with its predators or other types of danger, such as disturbance stimuli derived from human presence. Alarm calls are usually the first response to signal and deter the origin of disturbance. However, effort spent on anti-predator strategies can change a species time and energy budgets, reducing the allocation of resources in activities such as feeding and mating. If human disturbance resembles the pressure done by a predator – the risk-disturbance hypothesis – it should constitute a serious threat to a species survival. As such, we studied the impact of human disturbance to a population of the Sumatran orangutan *Pongo abelii*, one of the most endangered great ape species in the world. We studied a natural population that resides in a secondary forest targeted for logging programmes and other human related activities, within the most important National Park in Indonesia – the Gunung Leuser National Park. We focused on recording orangutan vocalizations, analysing especially alarm calls towards human observers (a group of researchers and guides). During most of the days following the orangutans they produced vocalizations, the majority of which were, indeed, alarm calls. Despite a certain degree of habituation, we found evidence that orangutans' call effort was similar or even greater than the effort they employ when facing their natural predator, the Sumatran tiger. These findings suggest that besides human pressure on orangutans' habitat, human presence has also a significant impact on the species daily activities, constituting an additional threat to its survival.

Keywords: Orangutan, vocalizations, risk-disturbance hypothesis, human disturbance, conservation

Communications

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(Poster)

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1. Introduction

1.1. Biodiversity loss and great apes

Great apes, our closest living relatives, are amongst the most threatened animal species in the planet (WWF 2017). As biodiversity and ecosystem services decay steeply, and remarkably high extinction rates are acknowledged worldwide in recent decades (Pimm et al. 2014), great apes follow along this trend.

Despite interest in hominids being not recent (e.g. Leyton & Sherrington 1917; Yerkes & Yerkes 1928; Coolidge 1933; Verhaart 1956; Donisthorpe 1958; Groves 1970), and continues today (e.g. Lameira et al. 2017; Galbany et al. 2017; Whiten 2017; Molnar et al. 2017), their natural populations continue to decline at a rapid pace contrasting with the hasty growth of an increasingly wealthy and demanding human population. Chimpanzees *Pan troglodytes*, bonobos *Pan paniscus* and gorillas *Gorilla* spp., in Africa, and orangutans *Pongo* spp., in Asia, are currently considered endangered of extinction (IUCN 2017). Forest loss, land conversion, poaching and illegal trading are some of the major drivers responsible for the deterioration of great ape populations, and wildlife in general, accompanied by a poor enforcement of laws and a poor environmental education and awareness across the globe, with an emphasis on developing countries with fewer resources and lower education rates.

Forests, home to 80% of the world's terrestrial biodiversity (Whelan et al. 2008; WWF 2017), have undergone a steep decrease in area across continents with a total of 230 million hectares destroyed between 2000 and 2012 (Hansen et al. 2013) due to human disturbances. Tropical forests are the most affected by these disturbances – around 5.8 million hectares of humid tropical forest alone were lost each year from 1990 to 1997 (Achard 2002), as they represent the highest ratio of forest loss in the world – 2101 km^2/year (Hansen et al. 2013). This forest removal translates in land conversion, in most cases due to the development of crops to meet social and economic demands.

Land conversion changes native habitats into a humanized matrix (non-habitat), ultimately causing fragmentation at different scales, through the creation of other land cover types and altering the landscape functional connectivity – constraining movement rate of individuals across the landscape (Pascual-Hortal & Saura 2006). This fragmentation not only breaks some of the functions inherent to a healthy natural system but also promotes direct contact between humans and many species that inhabit native patches. This implies disturbance of the daily basic activities of a different number of species - such as foraging, searching for mates and hiding from predators (Frid & Dill 2002), but also implicates the loss of basic human resources – cattle predation for instance, due to increased vulnerability to top-predators – upon which many people depend (Polisar et al. 2003; Madhusudan 2003), thus bringing extra difficulties for Conservation programmes and environmental care and awareness. Another interference that is promoted and facilitated by habitat destruction and fragmentation, with serious impact on wildlife, is poaching (Kenney et al. 1995; Robinson & Bennett 2004; Harris et al. 2009; Waltert et al. 2009; Pimm et al. 2015). Poaching feeds the illegal trading markets, which later promote the increase in the number of poachers, as both activities are far more profitable for locals than most others, being only deterred at very high levels of law enforcement (Milner-Gulland & Leader-Williams 1992), as shown in Ghana, able to reduce illegal ivory trade (Martin 2010). Even though many species are protected by law, corruption, poor enforcement of rules and weak compliance of these regulations creates opportunities for these activities to continue at a steady pace (Robertson & van Schaik 2001).

1.2. Forests and biodiversity in Southeast Asia and the island of Sumatra

One region of the globe where human actions are not only intense but regular – a result of the pronounced population growth and inevitable disturbance (Gaveau et al. 2007) – is Southeast Asia, where prime conditions for the maintenance of several human-dependent crops, such as oil palm *Elaeis guineensis* or rice *Oryza sativa*, persist (Pardey et al. 1992). This makes these areas especially vulnerable to deforestation, destruction of other natural systems and removal of key elements from the ecosystem, ultimately affecting animal biodiversity (Rerkasem et al. 2009). This region of the globe faces the highest deforestation rate of any other tropical region (Sodhi et al. 2004), which can lead to a decay in 42% of its original biodiversity by 2100 (Sodhi et al. 2004). Vast countries such as Indonesia, with extended lowland forests, are on the frontline of Conservation concerns, as their forest loss ratio has even surpassed countries with the previously highest deforestation rates, such as Brazil (Margono et al. 2014). With forests covering 87% of its territory in 1950 (Tsujino et al. 2016), Indonesia has removed 68 Mha of tree cover from then until 2015 to make way for arable land (12.7 Mha), permanent crops (22.3 Mha) and other land uses (around 33 Mha) (Tsujino et al. 2016). This resulted in a territory currently covered by only 25% of native forest (Tsujino et al. 2016). The removal of vegetation from lowlands and peat-swamps, ideal for agricultural purposes, affects not only local flora and fauna but also its role in sequestering and storaging carbon stocks, as well as in regulating regional hydrological cycles (Wich et al. 2016), from which many villages depend, as they are generally located bellow natural forests (Tata et al., 2010). Unfortunately, one of the Indonesian islands most affected by these events – the Sumatra Island – is also one of the most biodiversity-rich, holding, for example, more mammal species than any other island (Kinnaird et al. 2003).

Sumatra, the largest island of the Indonesian Archipelago, with 164,000 square miles, is one of the most important parts of the Sundaland Biodiversity Hotspot, which comprises the islands of Sumatra, Borneo, Java and the Malaysian Peninsula (Myers et al. 2000). Together with Wallacea, Indo-Burma and the Philippines hotspots, they include 17,000 islands along the Equator, between Asia and Australia, making this region one of the richest hotspot systems in the world – home to 10% of the world's know plant species, 12% of mammals, 17% of birds, 16% of reptiles and amphibians and 25% of fish (Fund 2001), many of which are dependent on lowland forest ecosystems (Payne 1985). Primary forests in Sumatra are disappearing at an alarming rate – 6.02 Mha from 2002 to 2012 with an average increase of 47,600 ha per year (Margono et al. 2014). This is due to forest fires (Sunderlin 1999; Barber & Shweithelm 2000; Robertson & van Schaik 2001; Holmes 2002) and mostly to legal and illegal logging (Gaveau et al. 2007; Margono et al. 2014; Wich et al. 2016), and the development of estate crops – such as sugarcane *Saccharum officinarum*, ruber tree *Hevea brasiliensis* and oil palm, the latter having a robust global market for oil and biodiesel (Swarna Nantha & Tisdell 2009). These activities affect directly some of Sumatra's most emblematic fauna, such as the Sumatran rhinoceros *Dicerorhinus sumatrensis*, the Sumatran elephant *Elephas maximus sumatranus*, the Malayan tapir *Tapir indicus*, the serow *Capricornis sumatraensis*, gibbons *Hylobates spp*, the sun bear *Helarctos malayanus* and eight species of felids, most notably the endemic Sumatran tiger *Panthera tigris sumatrae* (Kinnaird et al. 2003). Sumatra is also home of the Sumatran tiger's prime prey, one of our closest relatives and the focus of this thesis – the orangutan, more specifically, the Sumatran orangutan *Pongo abelii* Lesson, 1827.

1.3. Orangutans: knowledge state of art and the risk of losing Asia's reddish great ape

Orangutans, the earliest diverging great ape lineage (Lameira et al. 2017), are the only living great apes whose distribution does not meet the African domain (Delgado & Van Schaik 2000; Wich et al. 2008). While currently distributed over Indonesia and Malaysia – more specifically the islands of Sumatra and Borneo (Rijksen & Meijaard 1999; Singleton et al. 2004) – orangutans had a wider distribution throughout the Pleistocene, ranging from southern China to the south of Java Island in Indonesia (von Koeningswald 1982; Bacon & Long 2001). They are the last living species of the sub-family *Ponginae*, which also hosted the biggest ape species ever known to man – *Gigantopithecus blacki* (von Koenigswald 1935) – which became extinct approximately 100,000 years ago (Bocherens et al. 2017).

Orangutans are reddish large-bodied frugivorous apes (Harvey et al. 1987) that live in a fission-fusion society (Delgado & Van Schaik 2000), where mating interactions range from brief encounters to courtships lasting for several days (Utami Atmoko et al. 2008). They are a highly sexual dimorphic species, as males can grow up to 78 kg or more, while females usually have around half of male's body mass (up to 36 kg). Some males can additionally develop a throat sac and flanges, a secondary sexual development characteristic that – allowing the distinction between flanged and unflanged males – foments the production of long-calls (MacKinnon 1971). Males' home range usually overlap with several female territories, which are philopatric, occupying the same area as their mothers did (Rodman 1973; Rijksen 1978). Females do not gain secondary sexual characteristics during their development, not even any signs of oestrus during their sexually receptive periods, like genital swelling (Delgado & Van Schaik 2000) as found for example in chimpanzees (Wallis 1992). Orangutans usually move alone through the forest by brachiating in the canopy – though they can also move on the ground (person. obs.) – a behaviour which has been associated with the substantial fluctuation in fruit availability of Southeast Asian forests (Knott 1998). This fluctuation may explain why orangutans forage alone and is in accordance with observations made in the wild (anecdotal obs.), where orangutans seem to have more encounters during prime fruit season. These encounters are called parties (van Schaik 1999) and are more common in Sumatra than in Borneo (van Schaik 1999). This may have to do with the fact that fruit is more available in Sumatra (Wich et al. 2006), as forest productivity is higher as a result of its less eroded volcanic rocks (MacKinnon et al. 1997), increasing soil fertility. Orangutans rarely go down to the ground in Sumatra in comparison to Borneo maybe due to the local extinction of the orangutans' natural predator, the Sumatran tiger (Rijksen 1978). Female orangutans hold the biggest interval between births in all hominids – 9 years (Wich et al. 2004) – which makes the longest generation length amongst the remaining great apes (Wich et al. 2008).

Orangutans were first considered to be two different sub-species: *Pongo pygmaeus abelii* in the island of Sumatra and *Pongo pygmaeus pygmaeus* in the island of (Caccone & Powell 1989; Zhi et al. 1996; Delgado & Van Schaik 2000). Even though there are many resemblances regarding behaviour and morphological features, or even the fact that they can cross-breed to produce fertile offspring (Muir et al. 1995), they are however further apart genetically than the two species of chimpanzees (Zhi et al. 1996), the common chimpanzee *Pan troglodytes* and the bonobo *Pan paniscus*, leading the recognition of two species – *Pongo abelli* in Sumatra and *Pongo pygmaeus* in Borneo (Xu & Arnason 1996; Groves 2001; Singleton et al. 2004; Brandon-Jones et al. 2004). Even though orangutans are protected by the Indonesian Law No. 5 (1990), regarding conservation of natural resources and their ecosystems, and Government Regulation No. 7 (1999), regarding diversity preservation of plants and animals (Tata et al.

2010), both orangutan species are considered Critically Endangered (IUCN 2017) despite having different population sizes.

For the Bornean orangutan *Pongo pygmaeus*, three different subspecies have been meanwhile recognized – *P. p. pygmaeus*, *P.p. wurmbii* and *P.p. morio* (Groves 2001). The first sub-species is considered the most vulnerable of all three, as estimates point to only 3,000 - 4,500 individuals inhabiting North-west Borneo (Wich et al. 2008). *P. p. wurmbii* is the most abundant one with an estimate of around 35,000 individuals living in Central Kalimantan, Borneo. The other sub-species, *P. p. morio*, persists in smaller populations in East Kalimantan (c. 4,800 individuals) and in Sabah, a Malaysian state of the Borneo Island (c. 11,000 individuals). Thus, in 2008 at least, the Bornean orangutan population was composed of 54,000 individuals (Wich et al. 2008).

The Sumatran orangutan population is far more depleted than that of its sister species, as past studies suggested that there were only 6,500 individuals persisting in the wild (Wich et al. 2008). However, recent estimates now suggest that there are around 14,613 individuals left in Sumatra (Wich et al. 2016), and the previous underestimation was a result of orangutans living at elevations higher than originally thought possible, unexpectedly using logged forests and found also at Toba Lake, a location never before surveyed for orangutans (Wich et al. 2016). Although abundance estimates seem to have improved from an earlier pessimistic view, orangutans are still at the mercy of human disturbance and habitat destruction. As S. Wich (2016) demonstrated, high human population densities affect orangutan densities. Poaching, for example, increases near to villages (Marshall et al. 2006) as they are often found to crop raid farms in the search for food. This explains why most Sumatran orangutans are now found within the boundaries of the Leuser Ecosystem (Robertson & van Schaik 2001; Wich et al. 2008), their ultimate stronghold on the island of Sumatra. This area is most suitable for orangutans as it holds a forest gradient from swamp forests and lowland forests – where orangutans are generally found at higher densities – to sub-montane forests at around 1000m (Wich et al. 2003; Wich et al. 2008).

The Sumatran orangutan suffers greatly from illegal poaching and pet trade (Rijksen & Meijaard 1999; Marshall et al. 2006), forest loss (Wich et al. 2008) – both within protected and unprotected forests (Wich et al. 2016) – and habitat fragmentation (Robertson & van Schaik 2001), which promotes crop raiding and adds more complexity towards conservation action. Though the killing of orangutans is acknowledged as one of the specie's major threats (Marshall et al. 2006) – a practice with tens of thousands of years (Schoneveld-de Lange et al. 2016) – there is no visible implementation of anti-killing strategies (Schoneveld-de Lange et al. 2016), as large suitable areas for orangutans are now found to be empty. Access improvement within forests, the increase of animal trade and an increase in human demand for resources difficult the implementation of an efficient conservation programme for this species (Wich et al. 2011). E. Meijard and colleagues (2011) published the first quantitative study on orangutan loss by poaching in Kalimantan, Borneo, and one year later S. Wich and his colleagues (2012) did a similar study in Sumatra. However, Indonesian officials do not recognize poaching as a serious threat for orangutans, this being a cultural-sensitive issue, as a big part of these killings occur for human feeding purposes (Davis et al. 2013). Forest removal and the continued conversion of remaining habitat for oil palm cultivation – the world's most consumed vegetable oil (Carter et al. 2007) – is also hastening its extinction in the wild (Swarna Nantha & Tisdell 2009).

Originally from Africa, oil palm was brought to Indonesia and Malaysia in the colonial period (World Growth 2011). As the demand for this oil persistently grew – mostly for its use in personal care products and as food oil (Swarna Nantha & Tisdell 2009) – so did the extension of the cultivated fields. From 1990 to 2006, it is estimated that at least 55% of the expansion of oil palm crops was done at the cost of natural forests (Koh & Wilcove 2008), impacting associated biodiversity. Although agriculture only contributes with 14% to Indonesian's GDP (World Growth 2011), it employs over 40% of its

population, as over half Indonesians live in rural areas (World Growth 2011). As demand for oil palm grows – it is expected to increase by 32% by 2020, resulting in a total of 60 million tons of oil palm per year (World Growth 2011) – limiting its production would take a significant impact on Indonesian socio-economy.

Although concerns about the impact of this monoculture are not new (e.g. Vries 1949) and continue to live on amongst conservationists and ecologists (e.g. Rist et al. 2010), government land-use planning decisions are not taking these into account. They forecast, on the contrary, the expansion of agriculture, which will most likely have serious negative impacts on the Sumatran orangutan (Robertson & van Schaik 2001; Singleton et al. 2004; Wich et al. 2011), as all land-use scenarios predict a decline in orangutan populations (Wich et al. 2016). Forests bellow 500m above sea level and peatland have been the most affected (Robertson & van Schaik 2001; Wich et al. 2011), as they are more suitable for the development of oil palm crops than steep mountainous regions. In addition to orangutans' life-history and behavioural ecology constrains – large body size, long inter-birth interval, typical low densities, large home ranges (P. Havery et al. 1987; Singleton & van Schaik 2001) – human disturbances, such as the ones described more extensively on section 1.1., oblige orangutans to live in increasingly restricted lowland rainforest fragments (Rijksen & Meijaard 1999; Wich et al. 2003; Singleton et al. 2004), making them extremely vulnerable to extinction (Leighton et al. 1995; Rijksen & Meijaard 1999; Singleton et al. 2004; Meijaard & Wich 2007).

1.4. Human-wildlife conflicts, animal communication and alarm calls

Therefore, as conflict between humans and wildlife increases, both in terms of space and resources (Woodroffe & Ginsberg 1998), the tools used by animals to adaptively respond to danger – may it be a natural predator, or an aggressive conspecific – become extremely important in the context of human disturbances as well. One of these tools are the species' communication systems, that is, the way animals transmit information, often signals, among each other (Kaplan 2014), including information about danger (N. Davies et al. 2012; Kaplan, 2014).

Off all types of communication – visual, acoustic, physical, olfactory, electrical, chemical, amongst others – acoustic information has been the target of many classic (P. Sherman 1977) and recent studies (e.g. Bílá et al. 2017; Kern et al. 2017; Yu et al. 2017). It is a key feature to understand the interaction dynamics of individuals or groups with their social environment. It can serve different purposes at a variety of different contexts, such as feeding (Bermejo et al., 1999), reproduction (Delgado 2006), competition (Slocombe & Zuberbühler 2007) and predation (Zuberbühler et al. 1999).

Alarm calls, in particular, are a type of acoustic information emitted when a potentially dangerous situation arises (P. Sherman 1977) that could menace an individual, a population or even a whole community (Zuberbühler 2016). Sources of danger could originate from aggressive conspecifics (e.g. dominance fights), or from predators and human intruders. By producing an alarm call, the sender of the signal allows receivers to seek for protection before the danger is too close, thus increasing the group's overall chances of survival – this is called prey manipulation (Charnov & Krebs 1975). It can also be used by the sender to call for help (Zuberbühler 2016), or to discourage aggressors from attacking, serving as an advertisement towards the aggressor that it has been seen – known as perception advertisement (Zuberbühler 2016). Alarm calling is also an important learning tool for less experienced individuals in a population (Curio et al. 1978; Zuberbühler 2016), allowing to increase the number of sentinels in the future, thus benefiting both the individual and the group.

However, alarm calling has also the general disadvantage of attracting the attention of the aggressor towards the caller (Maynard Smith 1965; Maynard Smith & Harper 2003; Kaplan 2014). This seemingly contradictory fact motivated the study of the adaptive value of such conspicuous signals that could differ depending on the degree of relatedness between the members of a group (Kaplan 2014; Zuberbühler 2016): if the social group is composed of non-kin (non-related individuals), the sender benefits from emitting the signal due to reciprocity, that is, from the alarm calls of the other members of the group (Trivers 1971); furthermore, if the sender is a male, it can also benefit from female mate choice, as females prefer mates that are willing to pay the risk of attracting the predator towards themselves, while providing protection to the female and her offspring (R. Seyfarth & Cheney 1990; Evans & P. Marler 1994; Zuberbühler 2016); if the social group is composed of kin (related individuals), the sender may also benefit from reciprocity, but the risk of being detected and eventually killed by the aggressor is mitigated by the high coefficient of relatedness that exists between kin (altruism: Hamilton 1963; P. Sherman 1977).

Alarm calls are a widespread phenomenon in the animal kingdom (Zuberbühler 2016), though more commonly described in birds (Møller 1988; Evans et al. 1993; Leavesley & Magrath 2005; Goodale & Kotagama 2008; Suzuki 2014) and mammals (Blumstein & Armitage 1997; Zuberbühler 2001; Manser et al. 2002; Murphy et al. 2013; Soltis et al. 2014). Additionally, it is interesting to see that even non-vocal animals, such as reptiles (Vitousek et al. 2007; Ito & Mori 2010), use alarm calls emitted by heterospecifics in the community to their advantage, hence being able to detect more accurately the source of potential danger. Yellow-casqued hornbills *Ceratogymna elata*, a sympatric bird species with the orangutan, also uses calls from other animals to respond to danger, being able to even distinguish between different primate alarm calls (Rainey et al. 2004). These discoveries seem to show a relevance of these signals beyond the species level, serving as helpful tools for all members of the community.

Nonetheless, time spent alarm calling – i.e., in a vigilant state – diverts animals from other fitness related tasks, such as foraging, looking for a mate, parental investment or habitat selection (Wich et al. 2016). The costs derived from such conflict, depending on whether the sources of danger are more or less frequent or persistent – chronic *versus* transient stress – will determine their impact on the wellbeing and conservation status of a given species or population. This is the risk-disturbance hypothesis (Frid & Dill 2002) that in the context of human disturbances is quite pertinent, given that human disturbance stimuli tend to be persistent and invasive.

1.4.1 The risk-disturbance hypothesis

The selection of a place to live, forage or mate is demarked by a trade-off between evaluation of predation risk and resource availability, as animals seek to be safe and maximize, at the same time, their energy intake and reproduction potential (Gilliam & Fraser 1987; Lima 1998). However, time spent diverting a given disturbance takes away time from other activities, making more difficult the acquisition of resources (Gutzwiller & Anderson 1994). This also affects parental investment, as predation risk influences not only the number of offspring that can be raised, but also the moment and place of reproduction (Magnhagen 1991). All these fitness related activities are fundamental towards the resilience of a species over time, having the potential to affect not only its population but the whole surrounding community (Frid & Dill 2002).

It is expected that animals respond to human disturbance stimuli in a similar fashion as they would in a predation context, following the same economic principles as encounters with predators

(Madsen 1994; Gill & Sutherland 2000; Frid & Dill 2002). Prey have developed, over time, responses to a widespread range of stimuli being more advantageous to overestimate the danger in any situation than otherwise (Frid & Dill 2002), as animals rarely have perfect information about the threat. However, predation risk and human disturbance stimuli differ in the aspect that predation is most of the times punctual or transient and human disturbance can be continuous or chronic, as fragmentation of habitat increases and native patches diminish in area, augmenting the contact rate with humans. The fact that individuals in a population will increase their time in a vigilant state due to these disturbances will subsequently affect their body condition over time and reduce their reproduction potential over long and intense disturbance stimuli – the risk-disturbance hypothesis – even increasing predation vulnerability (Frid & Dill 2002). This increase can lead to shifts in community structure, affecting both the density of prey and predators. This hypothesis gives, therefore, relevance to the need to understand how species deal with prolonged human disturbances.

Non-human primates in general, who are renowned for their diverse vocal repertoires, produce alarm calls in disturbing circumstances (Zuberbühler 2016), amongst other contexts (Hardus et al. 2009a). Although there has been a diverse array of primate studies focusing on alarm calls (Zuberbühler et al. 1999; Zuberbühler 2001; Esther Clarke, Ulrich Reichard 2006; Murphy et al. 2013; Schel et al. 2013) the chimpanzee *Pan troglodytes* has been the focus of most great ape vocalizations studies (Hardus et al. 2009a), more specifically their pant hoots (Mitani et al. 1999; Marshall et al. 1999). Results demonstrate that this type of sounds in *Pan troglodytes* are not an inadvertent response to distress, but that they are indeed produced with the intention (adaptive function) of communicating danger to others (Zuberbühler 2016). The vocal repertoires of other great apes are also fairly well known (bonobos: Bermejo & Omedes 1999; gorilla: Salmi et al. 2013; and orangutans: Hardus et al. 2009a), most studies focusing either on interactions with natural predators (Zuberbühler et al. 1999; Zuberbühler & Jenny 2002; Gil-da-Costa et al. 2003; Farris et al. 2014), or on call characterization, such as call structure (J. & Gros-Louis 1998; Hardus et al. 2009b; Lameira et al. 2013b), call culture evolution (Whiten 2000; Castro & Toro 2004; Wich et al. 2012) and language evolution (Arnold & Zuberbühler 2006; Lameira et al. 2014; Lameira et al. 2017). However, no study has yet investigated the impact of disturbance stimuli promoted by the presence and activity of humans on great apes' call rate and call effort, and how this response can subsequently affect their body condition and overall behaviour.

1.5. Orangutan vocalizations

Although orangutans are a solitary species, their acoustic communication play an important role in their survival, not only by helping to define territorial boundaries without physical confrontations, but also during direct interactions with conspecifics (e.g. mating encounters), or when facing a predator. Orangutans' natural predators are Sumatran tigers, and clouded leopards, *Neofelis diardi* (Rijksen 1978). When they alarm call towards them they exhibit stress and discomfort, as observed by the frequent branch throwing or sudden movements when calling (Rijksen 1978; Hardus et al. 2009a; Lameira et al. 2013a). When in captivity, these behaviours are also triggered by human disturbance stimuli, becoming useful proxies to measure their levels of wellbeing and stress (Boinski et al. 1999). As such, orangutan call rate in the wild as a response to human disturbance, could also prove to be an interesting tool to assess the disruption that human activities may represent to orangutans' wellbeing in their natural habitats, and its consequences to the species conservation status.

Orangutan vocal repertoire was first described by J. Mackinnon (1974), being updated in the following years, as field work effort and interest for the species vocal properties grew (Rijksen 1978;

Galdikas 1983; Mitani 1985; Delgado 2006). This lead to the richest vocal repertoire recorded to date in all non-human great apes, next to the bonobo *Pan paniscus* (Hardus et al. 2009a; Lameira et al. 2015). The most recent publication, reviewing and updating the orangutans' vocal repertoire, was published in 2009 by M. Hardus and her colleagues, comprising the description of 32 different calls and their functions. Immature individuals have been described to produce 10 of these calls, nulliparous females 12 and parous females 14. Among these, females have four unique call types: mating squeals, fear squeaks, lork call and roar (Hardus et al. 2009a). Unflanged males have the largest repertoire with 17 different calls, whereas flanged males emit 15 different calls, one of which is unique to this Age-sex class: the long-call (Delgado et al. 2009; Hardus et al. 2009a), which only occurs when males start developing their flanges, consequence of a secondary sexual development in the later stages of their growth (Mitani 1985; Galdikas & Insley 1988; Delgado et al. 2009). These are the loudest calls emitted by orangutans (Galdikas 1983), being heard as far as 1500m (Hardus et al. 2009a) and reaching three minutes or more in length (pers. obs.). It is also the most studied vocalization in the orangutan (Galdikas 1983; Delgado 2006; Lameira & Wich 2008; Askew & Morrogh-bernard 2016). This call is thought to serve different purposes: mediate dominance relationships between males (Galdikas 1983; Delgado & Van Schaik 2000), attract females (MacKinnon 1979; Galdikas 1983; Mitani 1985), and act as a cohesion mechanism for their fission-fusion society (Delgado & Van Schaik 2000).

Bearing in mind that orangutans spend most of their adult life alone, with few social encounters, it is likely that their alarm calls are of the perception advertisement type – to inform the predator that it has been seen – as most of the produced alarm calls are not suited for long distances. It appears therefore that alarm calling in orangutans is not used to warn other orangutans of the presence of danger, nor a cry for help – unlike other great ape species that even modify their alarm calling depending on its audience (Slocombe & Zuberbühler 2007) – but as a tool to directly confront danger. Nonetheless, they generally produce these vocalizations from high in the treetops (pers. obs.), since alarm calling not only informs the predator that it has been seen, but also that its prey is nearby (Maynard Smith 1965; Maynard Smith & Harper 2003; Kaplan 2014).

Orangutans can alarm call in two separate forms: using single syllables or combinations of syllables (Lameira et al. 2013a). The most common alarm call is the Kiss-Squeak (Lameira et al. 2013a), which is a one-syllable sharp intake of air with pursed trumpet-like lips that causes a sharp kiss sound (Hardus et al. 2009a). Other alarm calls, such as the Grumph (Lameira et al. 2015), an inhalatory belch-like one-syllable vocalization that can last up to two seconds (Hardus et al. 2009a), or the Gorkum, which is a bout of grumphs alternated by rolling calls (multi-syllable) (Hardus et al. 2009a), are common as well. Multi-syllable calls use different combination of syllables, mostly Kiss-Squeaks with another call (e.g. Kiss-Squeak + Grumph). They can become long sequences of calls when orangutans call from several minutes to more than an hour (Lameira et al. 2013a).

There are two other interesting features of orangutan calls: 1) individuals have been observed to use tools (Hardus et al. 2009b) or just their hands (de Boer et al. 2015) to modify the output of their calls. For instance, Kiss-Squeak Hand is a variation of the classic Kiss-Squeak where the hand is placed is front of the mouth to create a deeper and lower frequency call (Hardus et al. 2009b; de Boer et al. 2015). It has been described to fool other orangutans or predators (Lameira et al. 2013), because a lower frequency call would only be emitted by a large individual. This type of innovation seems to show how important these calls are and how inventive orangutans can be. And 2) orangutan syllables can either be voiceless calls – calls that do not require vocal-fold action – or voiced calls – those that require such motor function (Lameira et al. 2017). Voiced calls are characteristic of not only primates but all mammalian vocal systems, whereas voiceless calls are present in all great apes but not in all mammals (Lameira et al. 2017). Since orangutan calls are composed of both voiced and voiceless calls, researchers decided to pay especial attention to orangutans' vocalization abilities, as voiceless and voiced calls can

help study the emergence of proto-consonants and proto-vowels, respectively, (Lameira et al. 2017) and contribute to the better understanding of the origins of human language.

On a more ecological approach, A. Lameira and colleagues (2013) tested whether the predator guild of the orangutan influenced their call rate in Sumatra and Borneo. They tested both orangutan species and four alarm calls – Kiss-Squeaks, Grumphs, Gorkums and Complex Calls – as well as their possible multi-syllable combinations. They showed that orangutan call rate, whether in single syllables or combinations, opposed to other primates previously studied (Zuberbühler 2001; Fichtel & van Schaik 2006; Fichtel & Kappeler 2011; Kavanagh 2014): orangutans do not produce different alarm calls in the presence of different types of natural predators. In other words, they do not produce specialized calls, while vervet monkeys *Chlorocebus aethiops*, for example, produce different alarm calls to signal the presence of leopards, snakes and eagles (Seyfarth et al. 1980). This rejects another proposed idea – the predation pressure (Stephan & Zuberbuhler 2008), that suggests predation as the regulating mechanism for call complexity and diversity in primates (Zuberbühler et al. 1997, 1999; Zuberbühler 2001; Stephan & Zuberbuhler 2008; Murphy et al. 2013) and mammals (Soltis et al. 2014) in general. Such unspecialized alarm calls in orangutans may have to do, as suggested by A. Lameira and colleagues (2013), with the relative bigger overall size of orangutans when compared with smaller primates, diminishing the number of natural predators. However, call rate on predator response shows an enormous flexibility between different orangutan populations (Lameira et al. 2013a), suggesting that this variability could be driven by specific causes, such as type of predator and/or predator abundance. Other apes such as chimpanzees also show a huge vocal flexibility across their range (Mitani et al. 1992). Additionally, it has already been shown that chimpanzees have the potential to modify their calls – structure and rate – in areas where humans are present and threaten their survival (Hockings 2009; Hicks et al. 2013). This happens also in smaller primates such as vervet monkeys or spider monkeys *Ateles paniscus*, where call rate is altered in regions where they are heavily hunted or when raiding crops, meaning that their communication systems adapt to human presence and disturbance (M. Van Roosmalen 2008; Hicks et al. 2013).

Besides a great anthropological interest in orangutan vocalization abilities, studies about how orangutans use their vocal communication in the wild to cope with danger are much scarcer and focused on orangutan responses to the presence of their prime predators (Lameira et al. 2013a). No study to date has approached the alarm call response of orangutans in the presence of humans. Given the pressure that humans impose over these animals, it becomes vital to understand how human pressure affects their alarm state, and by consequence their disposition to spend time and energy in other fitness enhancing activities.

1.6. Question and predictions

As conflict between Sumatran orangutans and human populations seems to increase – much due to crop-raiding (Marchal et al. 2009; Campbell-Smith et al. 2010) and poaching (Marshall et al. 2006; Corlett 2007) – it becomes imperative to study the orange great ape on a disturbance stimuli context. By causing chronic risk avoidance behaviours, human-derived disturbances can indirectly affect the fitness and population dynamics of this species (Frid & Dill 2002), by decreasing well-being and diverting time from activities such as feeding, parental care or mating encounters and displays – the risk-disturbance hypothesis (Frid & Dill 2002). With all this in mind, this master thesis aimed at addressing the effect of human disturbance stimuli on orangutans, namely how it influences alarm call rate, effort and variability (as both syllables and syllable combinations) of the Sumatran orangutan in one of the largest and most important National parks of Indonesia – the Gunung Leuser National Park.

With this aim, we addressed the following questions:

1) Do orangutans direct vocalizations towards humans?
2) Are most of these vocalizations alarm calls?
3) Are there alarm calls most frequently used to signal human presence?
4) Is there a decrease in alarm call rate due to habituation to the human presence?
5) Does alarm call effort towards humans differ from orangutans' alarm call effort towards tigers?

Because the impact of humans at the Gunung Leuser National Park is known to be very severe (Robertson & van Schaik 2001) we expect that Sumatran orangutans living there react to human observers during field work campaigns and predict that orangutans directly vocalize towards the human observers, and that most of the vocalizations are alarm calls. Kiss-Squeaks are the alarm calls most commonly used by orangutans (Hardus et al. 2009a), so these are expected to be the most used to signal human presence, both as syllables (one call) and combinations (two calls combined). Alternatively, if Sumatran orangutans perceive the human presence as especially dangerous, we predict that they should more frequently employ Complex calls – which are vigorous intimidation displays (Hardus et al. 2009a) – in the presence of humans than other type of alarm calls. However, because human presence tend to be persistent, and we followed the same orangutans for several days, we also predict, as others had already suggested (Mackinnon 1974), a diminishment of alarm call rate through time as evidence of habituation. Finally, we expect that the overall alarm call effort towards humans – the frequency and time the orangutans spend calling in a stressing situation – should be at least similar (if not higher) to that employed towards predators. This would corroborate the main prediction of the risk disturbance hypothesis (Madsen 1994; Gill & Sutherland 2000; Frid & Dill 2002), highlighting that human disturbance stimuli is a form of predation risk that can negatively influence orangutans' time allocation relatively to other fitness related tasks and their well-being (Frid & Dill 2002).

2. Methods

2.1. Study area

This study was conducted from January to June 2014 – a nonmast fruiting period – at Sikundur Field Station (3˚55'48.07''98˚2'31.17''), which comprises a research area of approximately 4 km^2 located in the Gunung Leuser National Park, in North Sumatra, Indonesia.

Gunung Leuser National Park is one of the 51 National Parks present in Indonesia, as well as one of the first five protected areas in the country (Rijksen & Griffiths 1995). It straddles the border of both North Sumatra and Aceh provinces and was declared a National Park in 1980, forming together with both Bukit Barisan Selatan and Kerinci Seblat National Parks the Tropical Rainforest Heritage of Sumatra. (UNESCO 2017). It is regarded as an area of international interest for the conservation of its unique and endangered biota – such as the Sumatran orangutan, the Sumatran tiger, the Sumatran elephant and the Sumatran rhinoceros.

Sikundur research station is positioned eastwards from the Alas River, which crosses and divides the National Park along its North-South axis (Fig. 2.1).

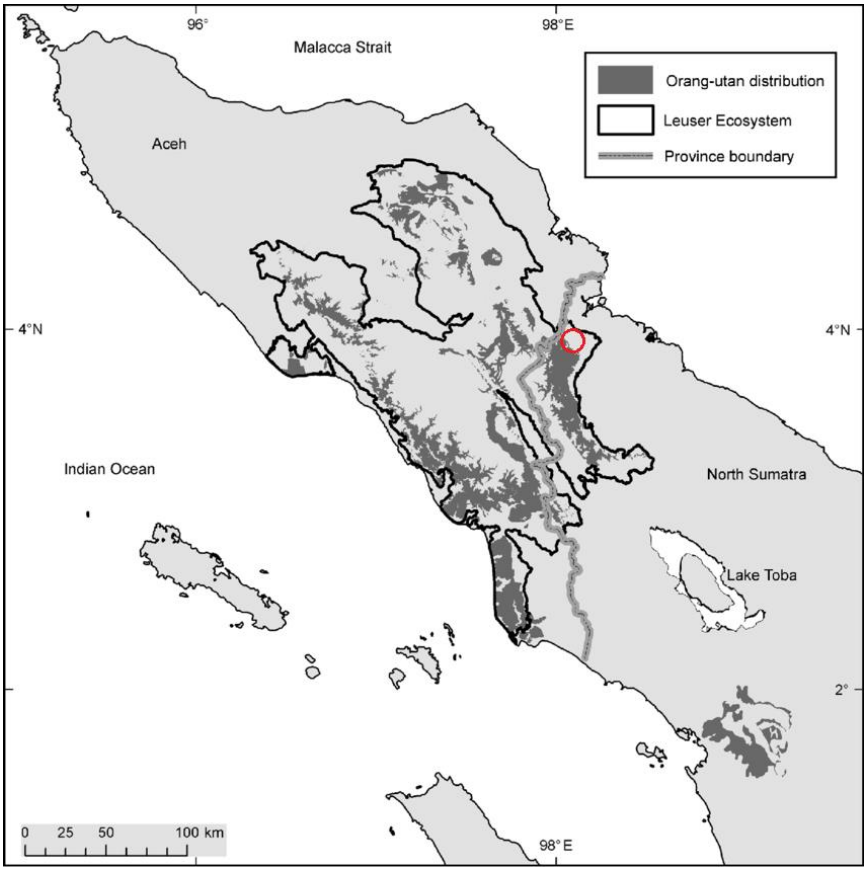

Fig. 2.1 Location of Sikundur Research Station (red circle), the Leuser Ecosystem and the Sumatran orangutan (in map, orang-utan) distribution at North Sumatra, Indonesia. Map from the PanEco report (2015).

This station is fairly recent, as the area where it is set was target of extensive logging programmes from the late 1970s until the early 1990s (PanEco 2015). This practice transformed a once pristine tropical forest into a complex and extended exploration of timber led by PT Raja Garuda Mas logging company, which ravished through the forest using machines and trails developed to aid the transportation of these resources outside Sikundur, reaching roughly 48km in extension.

In 2000, after the stop of the logging, the management of this area was granted to Leuser International Foundation (LIF) that implemented the Leuser Development Programme, a platform designed to oversee the North Sumatran portion of the Leuser Ecosystem. Back then, Dr. Eva Knop and Dr. Serge Wich surveyed for orangutans in the area for the first and only time before this thesis. Confirming the presence of some individuals during their campaign (PanEco 2015), they concluded that if conditions were met to support the continuous growth of the forest and its resources the area had potential to support once again a population of this species.

As the programme reached its end in 2004, LIF and the Leuser Management Unit continued to manage the area, with special focus towards Sumatran elephants. However, concerns about the status of orangutans in the area remained, motivating the partnership between a non-governmental agency, Sumatran Orangutan Conservation Programme (SOCP), the Frankfurt Zoological Society (FZS) and the Yayasan Ekosistem Letari (YEL). The partnership's primary focus was the development of quarantines that would be adequate to manage confiscated illegal pets and help them be reintroduced into the wild. Nowadays, the new SOCP-YEL although maintaining this mission further extended its lines of action, having currently over 70 local staff members distributed across Sumatra – not only in Sikundur but also in Ketambe and Suaq. They now focus their attention on the preservation and conservation of viable wild populations of the Sumatran orangutans, dealing with a reality where human-orangutan conflict is growing as their native forests continue to disappear in favour of the overgrowth of the human population.

At present, SOCP-YEL is acknowledged as the main reference in what concerns the status of the Sumatran orangutan populations. After almost 20 years of recovery, Sikundur is now a secondary forest, mainly characterized by a lowland dipterocarp tropical rainforest over mineral soils (PanEco 2015), with some steeper areas. It is surrounded by open forest, except in the south where the limit is the Besitang a river, with orangutans being completely free to move within the area and across its borders (Fig. 2.2).

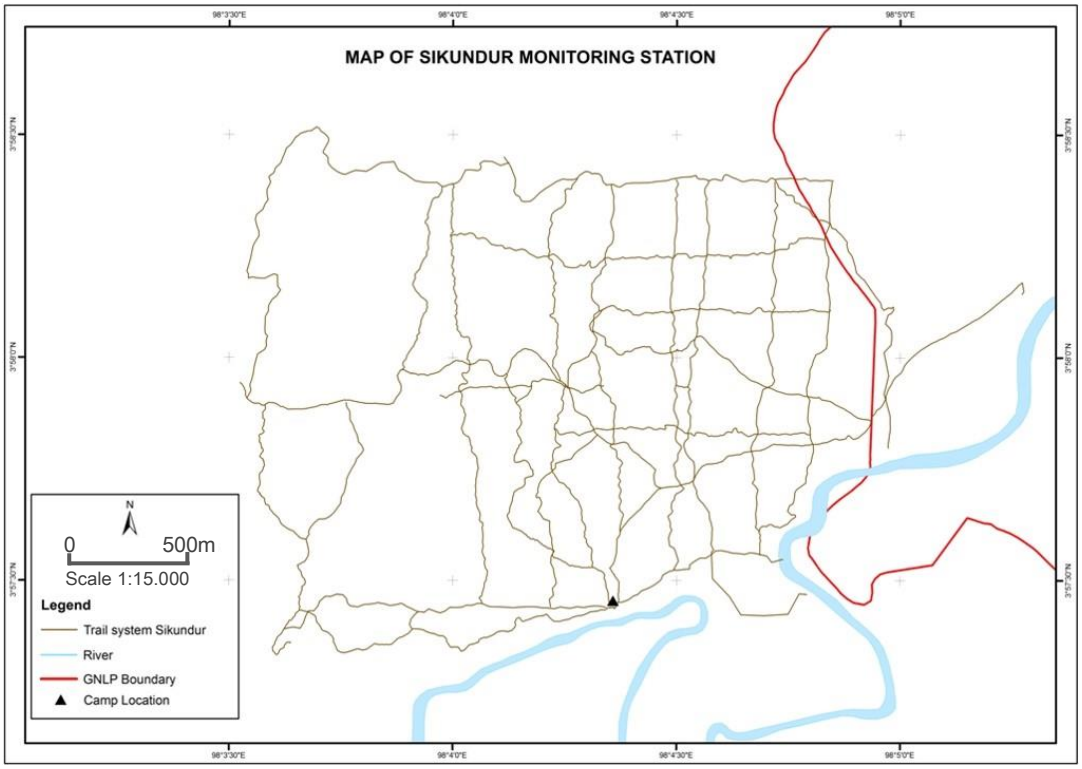

Fig. 2.2 Limits and trail network within Sikundur monitoring station. Map provided by M. Nowak from SOCP-YEL.

SOCP-YEL maintains six permanent field staff members at the station since 2013, in order to monitor the status of the orangutan population and to control for any furtive hunters or collectors of natural resources entering the area. Unfortunately, these events are still common. I observed more than once people trying to collect birds to sell in black markets and cut down trees in a protected area to plant fruit trees that would benefit not only local villages but also corporations. Corporations entice local people for these activities with low but valuable salaries, resulting in the destruction of the native forest. Hence, if it were not for the work developed by organizations such as SOCP-YEL, the Sumatran orangutan would probably have been lost a long time ago.

2.2. Data collection

The methodology used for data collection was not designed to directly answer to the questions of the present thesis. In the next two sections we explain the goal of the original research and how did we extract the necessary information from the collected data to evaluate the impact of human presence in the Sumatran orangutan alarm call rate, effort and variability.

2.2.1. The "Language Evolution" project field protocol

The methodology here applied was designed by Dr. Adriano Lameira from the University of St. Andrews, Scotland, and overseen by Professor Serge Wich, from LJMU, England. I and Raquel Vicente, alongside with SOCP-YEL local staff members set at the research station, were responsible for implementing the field procedures and acquire data on the orangutan natural population.

The goals of Dr Adriano Lameira project were (1) to characterize the vocal repertoire of the orangutan population of Sikundur, (2) increase knowledge about the Sumatran orangutan overall call panorama and (3) contribute to the basic understanding of the evolution of human language through the compilation and analysis of orangutan's voiced-calls (proto-vowels) and voiceless-calls (proto-consonants) as to determine how these calls came to evolve to our current vowels and consonants. Several other research stations had already contributed with data from the vocal repertoire of local orangutan populations – mostly by Dr. Adriano Lameira – but this had never been done for this specific research station.

In order to do so, our team divided in two survey groups (each with one of us – I and Raquel Vicente – and some members of SOCP-YEL) to increase our chances of finding and follow individual orangutans. Orangutans live in fission-fusion communities (Delgado and Van Schaik 2000), where individuals roam through the forest, most of the time alone, with the exception of females which carry their offspring until they are around 6 years old (Wich et al. 2004). This makes sampling orangutans a harder task than sampling other great apes that live in groups and have a well-marked territory. It is relevant to state that there was no interaction or handling of these animals during the study – strictly following the Indonesian law – thus promoting orangutan's free will and a data set that reflects natural circumstances as close as possible. When an orangutan was found, we followed him/her until nightfall, which is the moment when they build a nest in a tree so that they can rest throughout the night. Each day thus corresponded to a sampling session.

Whenever an individual was detected, its GPS position was recorded as well that of the trail forest used in order to allow us to return to the same nest the following day, just before the orangutan woke up – usually between 5 a.m. and 6 a.m. – and continue recording his/her behaviour in a new sampling session. Identifying the individuals was sometimes a tricky challenge, so we relied upon photographs previously taken by Professor Wich, and Dr. Knop and upon SOCP-YEL staff's experience.

Wild Sumatran orangutan calls were recorded at a distance between 10 to 20 m from the focal individual and categorized accordingly to orangutan's known vocal repertoire (Hardus et al. 2009a). Hence, within each sampling session (day), several audio recordings were made. All audio recordings were collected from focal animals or from focal groups – conspecifics in association, called parties. When there was a party, calls from every individual in the group were recorded simultaneously. This means that these animals shared the same recording time.

Calls were recorded using a Marantz Analogue Recorder PMD-660 (Marantz, Corporation, Kenagawa, Japan), a ZOOM H4next Handy Recorder (ZOOM Corporation, Tokyo, Japan) and two RODE NTG-2 directional microphones (RØDE Microphones LLC, Sidney, Australia). Audio data were recorded under Wave format at 16 bit as to maximize the retention of information within the recordings. Calls that could not be recorded were identified and registered in recording sheets.

2.2.2. Protocol adaptation for the "Alarm calls" project

For this master thesis we followed the field protocol described in the previous section but for data handling purposes some adaptations were needed to fulfil the thesis goal. Therefore, from the available data set, we selected the sampling sessions with and without vocalizations and categorized the orangutan vocalizations as alarm and non-alarm calls. Additionally, we selected the alarm calls produced only by adult orangutans towards the human observers. Calls from infants were excluded as they never produced alarm calls towards humans, though they did call, mostly to their mothers. We also excluded

the alarm calls directed towards non-human animals. These could have been used as a comparison term with the alarm calls towards humans, but they were not numerous enough. Finally, we also excluded from the data set those alarm calls where the information about the target or context of the call was scarce, incomplete or dubious.

Four response variables were used to answer to the different questions of this research: 1. *Call presence* - binary variable, calculated from the number of sampling sessions with and without calls; 2. *Call frequency* - continuous variable, calculated by dividing the number of calls produced at each sampling session per the total duration (in hours) of the corresponding sampling session; 3. *Alarm call duration* - continuous variable, calculated from the mean duration (in seconds) of each call category – time between the beginning and ending of each call – multiplied by the total number of recorded calls of each category. Then, the call durations of each category were added up, giving a total call duration time for each sampling session; 4. *Alarm state duration* - continuous variable that quantifies the amount of time (in seconds) during which orangutans remained stressed – during and after the vocalizations – in the presence of the human observers at each sampling session. This was calculated based on the duration time of each audio recording file. The durations of each recording file were added up to obtain a total call state duration time for each sampling session.

If the orangutans were found in parties, the calls from each orangutan in the party were included in the data set. This means that the same sampling session appears in the data set more than once – one entry per each orangutan producing alarm calls in the party.

2.3. Data analysis

A Shapiro-Wilk test was conducted to verify whether the response variables "*Call frequency*", "*Alarm call duration*" and "*Alarm state duration*" were normally distributed or not ($p < 0.05$). As these variables presented a non-normal distribution, and given the fact that "*Call presence*" is a binary variable, nonparametric statistical analyses were conducted using R 3.3.2 (R Development Core Team 2017) and a cut-off for significance of 0.05. For each question formulated in the introduction we performed a different statistical analysis.

1) Do orangutans direct vocalizations towards humans?

Using the response variable "*Call presence*", we assessed whether sampling sessions with calls directed towards humans (alarm and non-alarm) versus without differed significantly. If yes, and if the frequency of sampling sessions with calls was higher than the frequency without, this would suggest that orangutan call production is significantly affected by the human presence. We tested this with a one-sample test for categorical binary data (proportion test), comparing our data with the null hypothesis of equal 0.5 probability of alarm and non-alarm calls.

To account for factors inducing behavioural variability on orangutans, "Gender", "Male-age class" and within a "Party" or not, were analysed to unveil how these explanatory variables also affected Call presence. To do so, we applied two-sample tests for equality of proportions to compare the sampling sessions with and without calls of "Males" versus "Females, of "Flanged males" versus "Unflanged males" and of "Party" versus "No-Party".

2) If yes, are most of these vocalizations alarm calls?

Using the response variable "Call frequency" and the explanatory variable "Call type" – with two forms, "Alarm" and "No alarm" – we assessed which calls orangutans used most frequently towards humans. If the frequency of alarm calls was significantly higher from that of non-alarms it would mean that humans trigger more often alarm responses from orangutans than not. As above, we also analysed the effect of "Gender", "Male-age class" and "Party" on the call frequency per hour. In order to do so, Wilcoxon-Mann-Whitney U-tests were applied for all the explanatory variables.

3) Are there alarm calls most frequently used to signal human presence?

Using once more the response variable "*Call frequency*", but now with a focus on alarm calls only, we did similar analyses as above to assess whether there were alarm call categories more frequently used by orangutans under the human presence. For this, we did a syllable and a syllable-combination analyses applying Kruskal-Wallis tests. For the syllable analysis, we used the explanatory variable "*Alarm call category*", which considers each syllable as one independent call. We chose to include in this data set alarm-call categories that the literature describes as being used by orangutans in the presence of their natural predators (leopards and tigers) (Lameira et al. 2013) and humans (Hardus et al. 2009a), plus the Kiss-Squeak Hand, – a variation of the classic Kiss-Squeak – making a total of five alarm calls: Complex Call, Grumph, Gorkum, Kiss-Squeak and the Kiss-Squeak Hand.

All five calls can be produced independently, however they are most of the time produced in combination with a Kiss-Squeak (Hardus et al. 2009a). Because call combinations play an important role in some known non-human primate alarm call systems (Esther Clarke & Ulrich Reichard 2006) and in orangutans, in particular (Lameira et al. 2013a), we did a syllable-combination analysis, taking into account the explanatory variable "Alarm call combinations". This variable considers that each call is constituted by a bout of syllables. It has five categories: Kiss-Squeak + Kiss-Squeak, Kiss-Squeak + Grumph, Kiss-Squeak + Gorkum, Kiss-Squeak Hand + Kiss Squeak Hand and Kiss-Squeak + Kiss-Squeak + Kiss-Squeak. These categories result from the combinations between alarm calls observed in the wild, as only one three-syllable combination was observed from possible 125 combinations (5^3) and only four two-syllable combination were observed from possible 25 combinations (5^2). Calls were considered in combination when the interval between them was less than one second.

4) Is there a decrease in alarm call rate due to habituation to the human presence?

As some individuals were followed for five days in a row, we tested if there was alarm call rate decay throughout the sampling sessions due to habituation. A Page's L trend test (Page 2016) for multiple comparisons between ordered data was conducted with the response variable "*Call frequency*" and the explanatory variable "*Sampling session*", to understand whether rank in sampling sessions affected the call rate.

5) Does the alarm call effort towards humans differ from orangutans' alarm call effort towards tigers?

Here, we employed Wilcoxon one-sample tests to compare our data with data from orangutan alarm call effort towards Sumatran tigers (to which we call "reference data"), which are orangutans' most important natural predator (Rijksen 1978; Lameira et al. 2013a). Our data include the response variables "*Alarm call frequency*", "*Alarm call duration*" and "*Alarm state duration*". As the overall amount of combinations was scarcer, hence difficult to accurately compare, we decided to only use alarm call syllables to run these analyses.

Alarm call frequency accounts for alarm call effort in terms of the number of times – and the corresponding energy that is spent – that orangutans are willing to signal to the predator or the human observer. Alarm call duration, on the other hand, accounts for the time investment of orangutans to calling. To obtain this variable we used 30 samples (or less if not available) of each alarm call category in order to retrieve their mean duration. To do so we used the recorded calls from the "Language Evolution" project and analysed them with Raven Interactive Sound Analysis Software (version 1.2.1, Cornel Lab of Ornithology, Ithaca, NY) – Window type: Hann; 3 dB filter bandwidth: 124Hz; grid frequency resolution: 2.69Hz; grid time resolution: 256 samples – following the procedures of previous studies (Hardus et al. 2009a). All recordings were recorded under WAVE/WAV format at 16 bit and transferred to a computer with a sampling rate of 44.1 kHz. Then, as explained above, for each sampling session we multiplied the mean duration of each call category by the total number of recorded calls in that category, and summed them up to obtain a total call duration time for each sampling session.

Finally, "*Alarm state duration*" accounts for orangutans' investment in a behavioural state of alarm that includes not only calling behaviour, but also a body posture and an attentional state towards the human or predator target. This means that the effort put in a state of alarm could be greater than the alarm call frequency or call duration alone. To account for this, we used the duration of each audio recordings (within each sampling session) to create this response variable, as each audio file corresponds to an alarm state by the focal orangutan. To achieve a more precise measurement, we removed the end portion of each file, because during the audio recordings we always waited for additional calls, which falsely added time to the true duration of an alarm state. The removal of these time intervals was standardized for all files, and based on the average duration of these intervals extracted from 30 randomly chosen audio files. Then, as explained previously, all recorded times were summed up to obtain a total call state duration time for each sampling session.

The reference data on orangutan behaviour towards tigers were obtained from a study by A. Lameira and colleagues (2013a), where focal female orangutans were exposed to a fake model of a tiger, which was «a realistic tiger-patterned sheet draped over a human demonstrator who is walking on fours». The model stopped in front of the females during two minutes and then moved until it was out of sight. The females' alarm call state response was monitored for 30 minutes (thought orangutans may remain in an alarm call state towards tigers for more than an hour; Hardus et al. 2009a; Lameira et al. 2013a) and the critical alarm call duration period was assessed to last 10 minutes. During that 10-minute period, the alarm call frequency was estimated to be 6.2 calls per minute and we considered this as our reference value to compare with the alarm call response of Sikundur orangutans towards the human observers. However, because these comparisons assume encounters with tigers at each sampling session, we corrected the tiger reference values from the A. Lameira and colleagues (2013a) study with the estimated tiger density for Sumatra. For this, we used the recent study (Sunarto et al. 2013) that estimates a density of 0.87 ± SE 0.33 tigers per 100 km2 (lower than 1.3 per 100 km2, estimated in 1994 by Griffiths). By adjusting this density to the Sikundur area of 4 km2, we obtained a density of 0.0348 tigers in Sikundur.

With this information, we then compared our "*Alarm frequency*" data with the corrected tiger reference value of 0.216 calls per minute (by multiplying 0.0348 tigers with 6.2 calls per minute); the "*Alarm call duration*" data with the corrected reference value of 0.348 minutes (by multiplying 0.0348 tigers with 10 minutes of call duration); and the "*Alarm state duration*" with the corrected reference value of 1.044 minutes (by multiplying 0.0348 tigers with 30 minutes of call state duration).

Our sampling methodology assumes a persistent encounter rate with humans (since our sampling sessions lasted for several hours each day and we were not able to get data for human density in the area), while tiger data represents a low per diem encounter rate with tigers. Both data are realistic. However, to compare the tiger reference data with only one encounter with humans, we repeated these analyses using a subset of our data: using alarm call responses from female orangutans only, from the first ten minutes of their alarm call response, and from their first call state of each follow period (because some females were followed for two or three periods of several consecutive days, we selected data from the first day of each follow period with a minimum of five days interval between each period).

3. Results

3.1. Sikundur orangutan population

During the 6 months field campaign for sampling wild orangutans at Sikundur field station resident females inhabiting the area and transient males were detected and followed, leading to a total of 10 adult orangutans and 3 infants. They were followed for a total of 1258 hours and 40 minutes – corresponding to 127 days/sampling sessions – during which 6260 calls towards the human observers were registered (Table 3.1).

Table 3.1 - Description of Sikundur's Orangutans, number of follow days and follow hours per individual. [a] Party orangutan, never followed as a focal individual. b Gave birth during the campaign, becoming a parous female near the end of the campaign.

Name	Gender	Age-sex class	Follow days	Follow time
Anto [a]	Male	Unflanged	2	16h05min
Bendot	Male	Unflanged	6	63h22min
Brutus	Male	Unflanged	14	135h43min
Irma	Female	Parous Adult	29	289h13min
James	Male	Flanged	2	19h34min
Kundur [a]	Male	Unflanged	2	16h05min
Madalena [b]	Female	Adult	21	218h21min
Ompung	Male	Flanged	15	152h15min
Suci	Female	Parous Adult	26	263h21min
Yanti	Female	Parous Adult	10	84h40min
Total	-	-	127	1258h40min

Of the 10 orangutans, 4 were unflanged males – Anto, Bendot, Brutus and Kundur –, 2 were flanged males – James and Ompung – and 4 were adult females – Irma, Suci, Yanti and Madalena. Of these, the first three were parous females, meaning that they were carrying offspring during the time of our observations (mothers of Irvan, Siboy and Yeni, respectively). As we found out later in the campaign, Madalena was pregnant of Malala, a female who was born somewhere between the end of May and the beginning of June, turning all females of this study into parous females at the later stages of this research.

Most of the orangutans that were followed matched earlier recordings from the first campaign (2000 and 2001), but some, such as Brutus, Anto and James, were considered new individuals in the population as they had never been detected before. The orangutans most followed throughout the new campaign were Irma and Suci, with 29 and 26 sampling sessions respectively. Anto, James and Kundur were followed only during 2 sampling sessions each (Table 3.1).

3.2. Do orangutans direct vocalizations towards humans?

From the total of 127 sampling sessions, 83 allowed recording calls directed to the human observers – alarm and non-alarm. Proportion tests showed significant differences between sessions with and without calls (one-sample proportions test: $\chi^2 = 11.37$, DF = 1, *P*-value = 0.0007; Table 3.2; Figure 3.1).

Table 3.2 - Summary statistics of the estimated proportions for call presence/absence for each explanatory variable. CI = Confidence interval [a] One-sample proportions test; [b] Two-sample test for equality of proportions. ·p < 0.05; *p < 0.01; **p < 0.001; ***p < 0.0001.

	N	**CI Max**	**CI Min**	**Estimated Proportion**	***P*-value**
Call presence [a]					
Presence	83	0.7342	0.5634	0.6535	0.0007 **
Absence	44	0.4365	0.2657	0.3464	
Call presence by gender [b]					
Female	46	0.6420	0.4246	0.53489	0.0001 **
Male	37	0.9683	0.7594	0.9024	
Call presence by Male-age class [b]					
Flanged male	16	0.9969	0.6924	0.9412	0.8655
Unflanged male	21	0.9671	0.6654	0.8750	
Call presence by Party [b]					
With Party	21	0.6447	0.3553	0.5000	0.0184 ·
Without Party	62	0.8174	0.6204	0.7294	

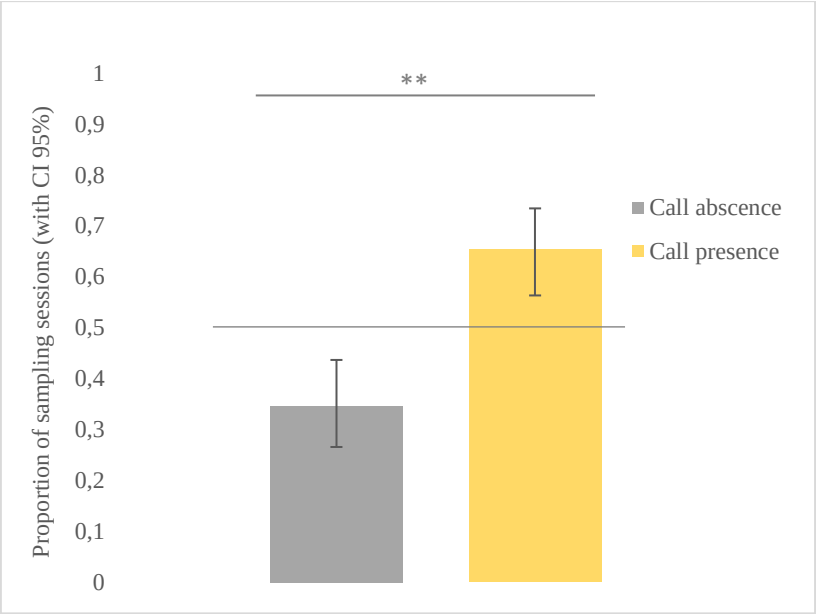

Fig. 3.1 Estimated proportion of sampling sessions with and without calls. Confidence intervals (CI) set at 95 %. **p < 0.001.

When analysing the factors inducing behavioural variability on orangutans, significant differences between the proportions of sampling sessions with and without calls were found at the gender (two-sample test for equality of proportions: χ^2= 14.982, DF = 1, *P*-value = 0.0001) and party (χ^2= 5.56, DF = 1, *P*-value = 0.0184) analyses; no significant differences were however observed between flanged and unflanged males (χ^2= 0.0287, DF = 1, *P*-value = 0.8655) (Table 3.2; Figure 3.2).

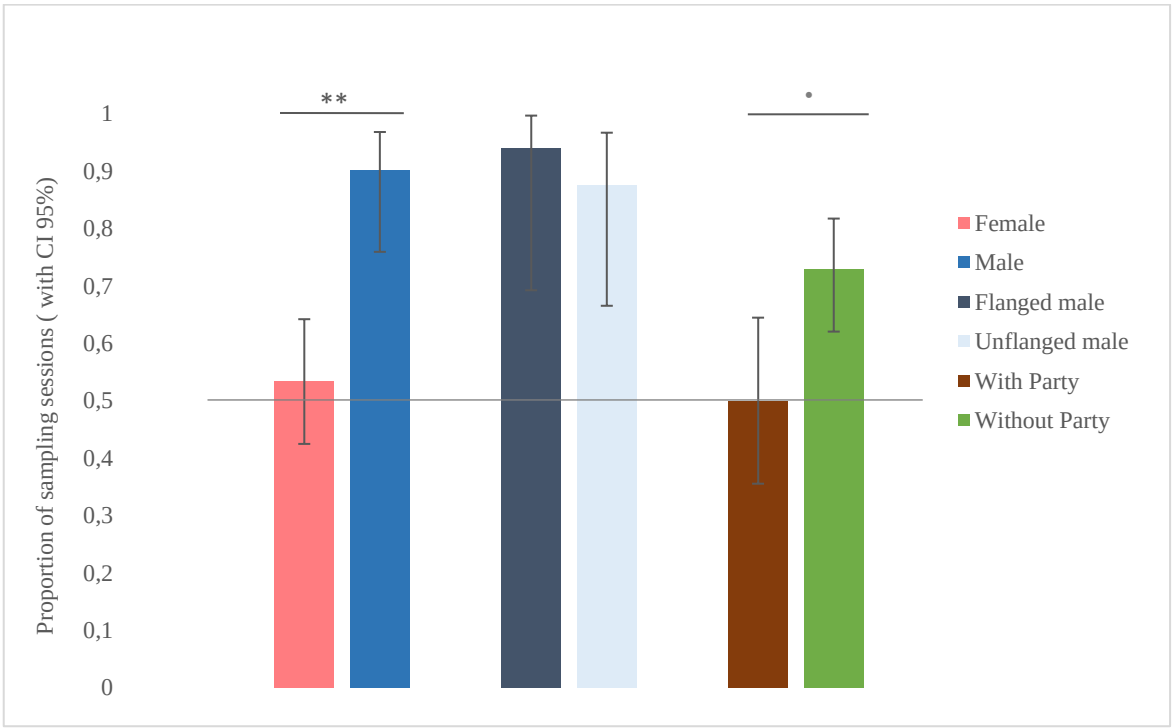

Fig. 3.2 Estimated proportion of sampling sessions with calls by Gender, Male-age class and Party. Confidence intervals (CI) set at 95 %. •p < 0.05; *p < 0.01.

Additional one-sample proportion tests were conducted on each behavioural class to understand whether orangutans in each class called more often in the presence of humans or not (Figure 3.2). The number of sampling sessions of females with and without calls was not significantly different (χ^2 = 0.2907, DF = 1, *P*-value = 0.5898), while that of males was (χ^2 = 24.976, DF = 1, *P*-value < 0.0001). Concordantly, both flanged (χ^2 = 11.529, DF = 1, p-value = 0.0007) and unflanged (χ^2 = 12.042, DF = 1, p-value = 0.0005) males produced more sampling sessions with calls. Finally, when orangutans formed parties, the number of sampling sessions with and without calls was not significantly different (χ^2 = 0, DF = 1, p-value = 1), while when orangutans did not form parties, the number of sampling sessions with and without calls was not significantly different (χ^2 = 16.988, df = 1, p-value < 0.0001).

3.3. Are most of these vocalizations alarm calls?

A total of 13 call categories were emitted in the presence of the human observers, and 6260 calls we registered (Table 3.3). The considered categories include one named "Any" that was created to accommodate the calls that we could not correctly identify as belonging to any of the other 12 categories. The average call per hour for the Sikundur orangutan population was 0.4320.

Table 3.3 - Summary statistics of all calls – alarm and non-alarm – registered towards the observers, with the respective median and mean call rate per hour. Q1 = First Quartile; Q3 = Third Quartile; SEM = Standard Error of the Mean. Calls such as Long-call or Fast-long-call have a lower valid N since only one Age-sex class (flanged males) can emit these calls.

Call category	Call type	Sessions N	No. of calls	Q1	Median	Q3	Mean	SEM
Any	Non-alarm	127	10	0	0	0	0.0066	0.0029
Complex call	Alarm	127	17	0	0	0	0.0125	0.0125
Chomping	Non-alarm.	127	39	0	0	0	0.0483	0.0271
Fast-long call	Non-alarm	41	3	0	0	0	0.0065	0.0048
Grumble	Non-alarm	127	1	0	0	0	0.0007	0.0007
Gorkum	Alarm	127	28	0	0	0	0.0249	0.0197
Grumph	Alarm	127	43	0	0	0	0.0381	0.0137
Grunt	Non-alarm	127	4	0	0	0	0.0045	0.0032
Kiss-Squeak	Alarm	127	5940	0	0.4934	3.9060	5.6425	1.3368
Kiss-Squeak Hand	Alarm	127	127	0	0	0	0.1153	0.0544
Long-call	Non-alarm	20	24	0	0	0.0808	0.1259	0.0716
Rolling call	Non-alarm	127	21	0	0	0	0.0156	0.0109
Throatscrape	Non-alarm	127	3	0	0	0	0.0027	0.0016

Among the alarm calls, Kiss-Squeaks were the most frequent type of calls, making over 94% of the total number of calls registered (5940 out of 6260). This results in a much higher call rate than the other calls – 5.6425 KSQs per hour (Table 3.3). Kiss-Squeak Hand was the second most registered call, with a total of 127 records, although with a much lesser call rate than the regular Kiss-Squeaks – 0.1153 calls per hour. All the other alarm calls, even non-alarm calls, have much lower number of recordings, making their call rates very low (Table 3.3).

Among the non-alarm calls, the studied population emitted calls such as Grunts towards the observers, though most of these calls were observed to occur between mothers and their offspring. Chomping or Chomps, a typical pre-fighting call emitted by males (Hardus et al. 2009a), was observed to be emitted by females in our population, especially by Yanti. And Throatscrape, a call emitted by females in a different number of circumstances (Hardus et al. 2009), was detected in males, namely in Ompung. Long-calls and fast long-calls, used at agonistic displays towards humans (Hardus et al. 2009a), were also recorded.

In the Sikundur orangutan population the mean frequency per hour of alarm calls was significantly higher than that of non-alarm calls (W = 226350, *P*-value = < 0.0001; Figure 3.3).

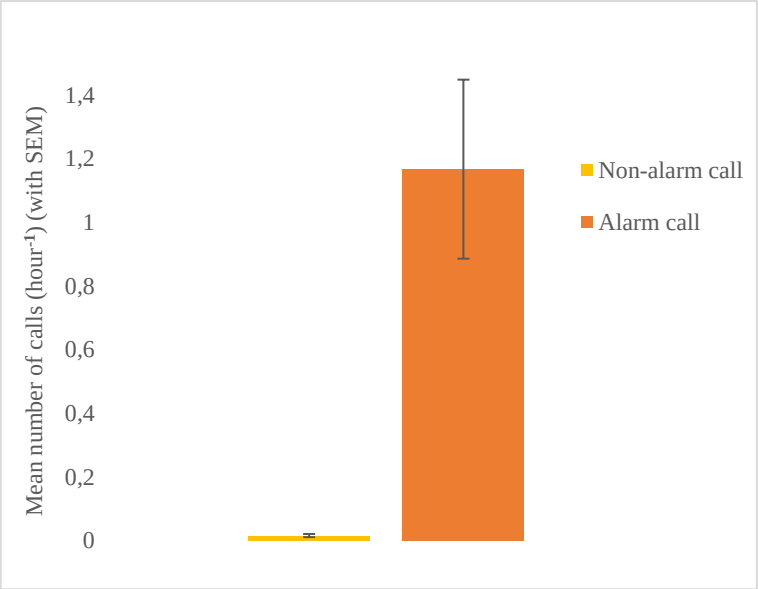

Fig. 3.3. Mean calls per hour for alarm and non-alarm calls, with standard error of the mean (SEM).

However, as the number of Kiss-Squeaks in our sample represents 94% of the total alarm calls recorded (Table 3 and Figure 3.4), we removed this call category from the analysis and found out that no significant difference occur between the mean frequency per hour of other alarm and non-alarm calls (W = 205380, *P*-value = 0.15; Figure 3.5).

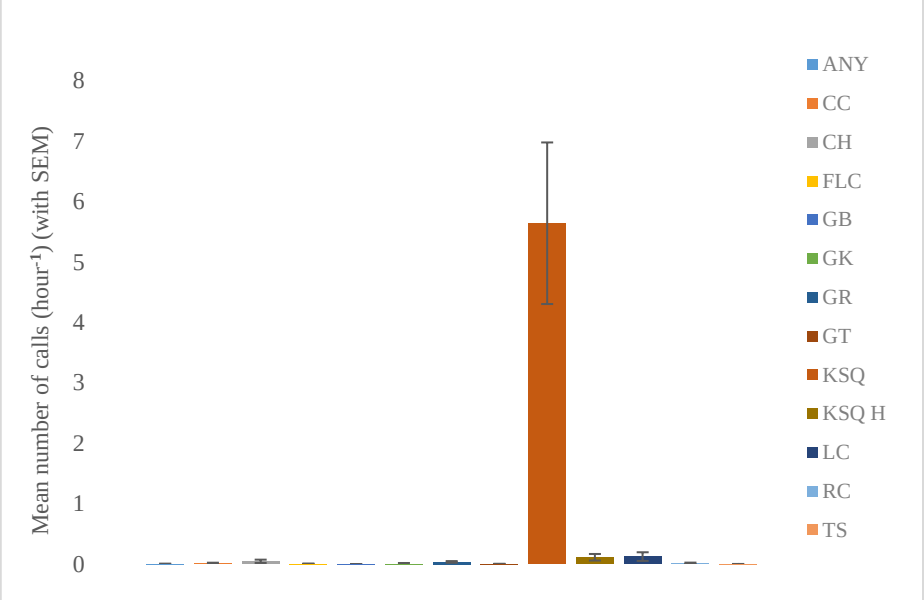

Fig. 3.4 Call repertoire towards the observers with all 13 different calls and respective mean calls per hour, with standard error of the mean (SEM). Calls' legend: ANY, Any call; CC, Complex Call; CH, Chomping; FLC, Fast Long Call; GB, Grumble; GK, Gorkum; GR, Grumph; GT, Grunt; KSQ, Kiss-Squeak; KSQ H, Kiss-Squeak Hand; LC, Long Call; RC, Rolling Call; TS, Throatscrape.

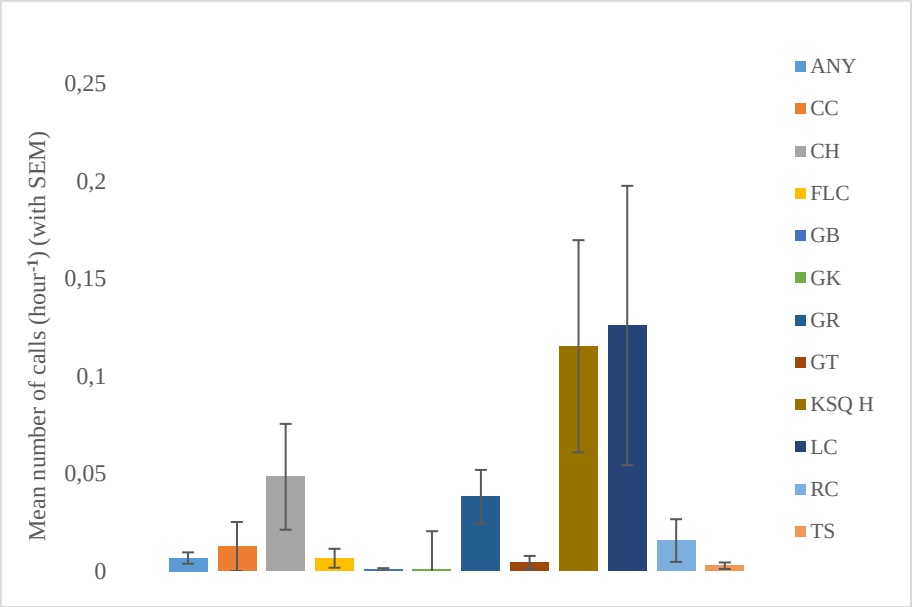

Fig. 3.5 Call repertoire towards the observers excluding the Kiss-Squeak call, with standard error of the mean (SEM). Calls' legend: ANY, Any call; CC, Complex Call; CH, Chomping; FLC, Fast Long Call; GB, Grumble; GK, Gorkum; GR, Grumph; GT, Grunt; KSQ H, Kiss-Squeak Hand; LC, Long Call; RC, Rolling Call; TS, Throatscrape

3.4. Are there alarm calls most frequently used to signal human presence?

3.4.1. Syllable analysis

From the total of 6260 calls emitted towards the observers, 98% (N=6153) were alarm call syllables. In agreement with the previous analysis, KSQ was the most frequent alarm call followed by KSQ Hand. The other three alarm calls – Grumph, Gorkum and Complex Call – accounted for only 88 (1.4%) of the total number of alarm calls (Table 3.4 and Figures 3.6 and 3.7).

Upon analysing the syllable alarm call rate by "Alarm call category", we found significant differences among the five call categories: Krukal-Wallis test. $\chi^2 = 246.58$, DF = 4, *P*-value < 0.0001 (see Table 3.4). Post-hoc comparisons showed however that the only true differences were that between KSQ and the other four alarm call syllables (Figures 3.6 and 3.7).

Table 3.4 - Summary statistics of the mean call rate per hour of the different alarm call syllables for each of the explanatory variables. SD = Standard Error; SEM = Standard Error of the Mean. •p < 0.05; *p < 0.01; **p < 0.001; ***p < 0.0001.

	N	**No. calls**	**Q1**	**Median**	**Q3**	**Mean**	**SEM**	***P*-value**
Call type								< 0.0001 ***
CC	127	17	0	0	0	0.0125	0.0125	
GK	127	28	0	0	0	0.0249	0.0197	
GR	127	43	0	0	0	0.0381	0.0137	
KSQ	127	5940	0	0.4934	3.906	5.6425	1.3368	
KSQ H	127	125	0	0	0	0.1138	0.0054	
Gender								0.0002 **
Female	430	4861	0	0	0	1.3527	0.3994	
Male	205	1292	0	0	0.0859	0.7756	0.2371	
Male-age class								0.4886
Flanged male	85	644	0	0	0.0931	0.9808	0.3982	
Unflanged	120	648	0	0	0	0.6302	0.2718	
Party								0.0332 •
No	425	5440	0	0	0	1.4291	0.3942	
Yes	210	713	0	0	0	0.6346	0.2921	

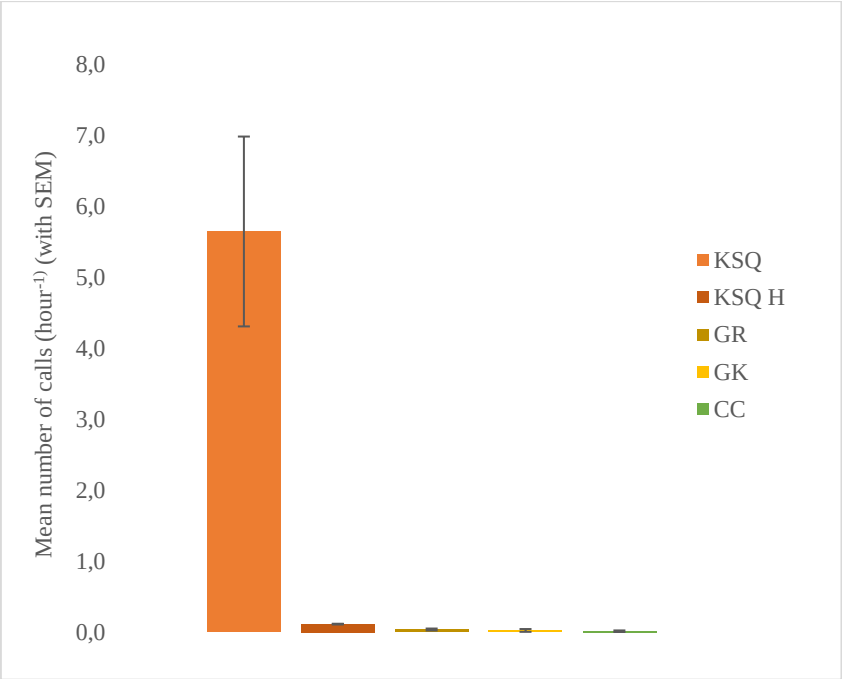

Fig. 3.6 Mean number of calls for all five alarm call syllables, with standard error of the mean (SEM).

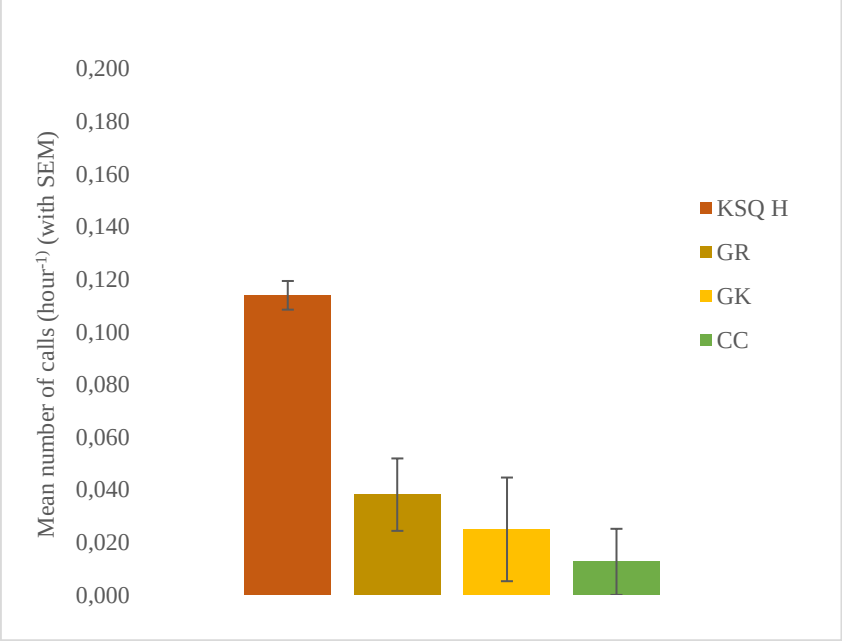

Fig. 3.7 Mean number of calls for all five alarm call syllables except KSQ – the most common call – with standard error of the mean (SEM).

The analyses considering the other explanatory variables (Mann-Whitney U-tests) accounting for the factors that induce behavioural variability, also showed significant statistical differences: Gender (W = 38916, *P*-value = 0.0003), Male-age class (W = 5322, *P*-value = 0.4886), and Party (W = 47657, *P*-value = 0.0332) (see Table 3.4 and Figure 3.8).

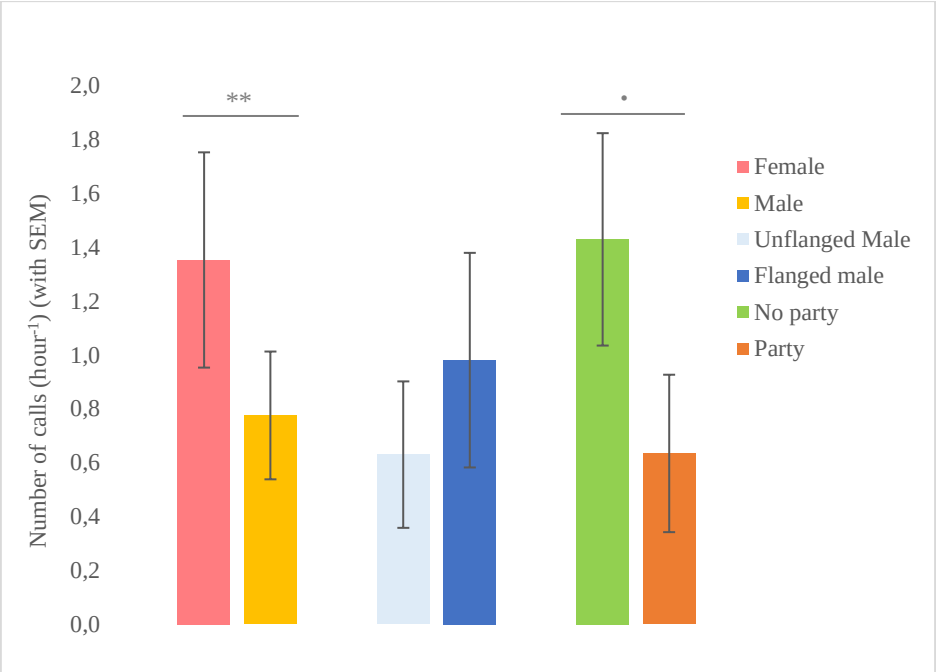

Fig. 3.8 - Mean syllable alarm calls per hour by Gender, Male-age class and Party, with standard error of the mean (SEM). •p < 0.05; **p < 0.001.

3.4.2. Syllable-combination analysis

The number of total alarm call syllable-combinations falls way behind the number of alarm call syllables registered during the field campaign. Throughout the sampling sessions only five alarm call syllable combinations were listened and registered for a total of 106 combination calls. By far the most common combinations were two-syllable combinations (such as Kiss-Squeak + Grumph), and only one three-syllable combination (KSQ + KSQ + KSQ) was registered (Table 3.5 and Figure 3.9).

Upon conducting the analysis of "Alarm call category" over the syllable-combination call rate, we found significant statistical differences between the five combination calls: Krukal-Wallis test. $\chi^2 = 9.637$, DF = 4, *P*-value = 0.0470 (Table 3.5). However, post-hoc analyses showed no true difference between any combinations.

Table 3.5 - Summary statistics of the mean call rate per hour of the different alarm call syllable- combinations for each of the explanatory variables. SD = Standard Error; SEM = Standard Error of the Mean. •p < 0.05; *p < 0.01; **p < 0.001; ***p < 0.0001.

	N	No. of calls	Q1	Median	Q3	Mean	SEM	*P*-value
Call type								0.0470 *
KSQ + KSQ	127	21	0	0	0	0.0163	0.0062	
KSQ + GR	127	38	0	0	0	0.0335	0.0139	
KSQ + GK	127	27	0	0	0	0.0244	0.0214	
KSQ H + KSQ H	127	19	0	0	0	0.0160	0.0090	
KSQ + KSQ + KSQ	127	1	0	0	0	0.0006	0.0006	
Gender								0.0139 •
Female	430	61	0	0	0	0.0157	0.0073	
Male	205	45	0	0	0	0.0233	0.0077	
Male-age class								0.8822
Flanged male	85	12	0	0	0	0.0213		
Unflanged male	120	33	0	0	0	0.0248		
Party								0.7766
No	425	76	0	0	0	0.0210	0.0079	
Yes	210	30	0	0	0	0.0123	0.0049	

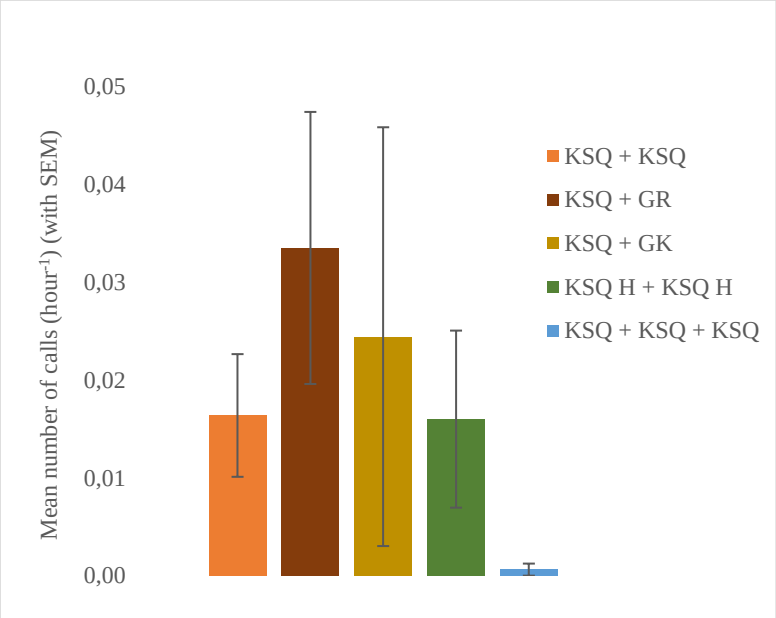

Fig. 3.9 Mean alarm call syllable-combinations per hour for all five categories, with standard error of the mean (SEM).

When addressing the influence of Gender, Male-age class and Party on the rate of syllable-combination calls, only Gender showed a statistically significant difference (W = 42184, *P*-value = 0.0139; Male-age class: W = 5071.5, *P*-value = 0.8822; Party: W = 44405, *P*-value = 0.7766) (See Table 3.5 and Figure 3.10).

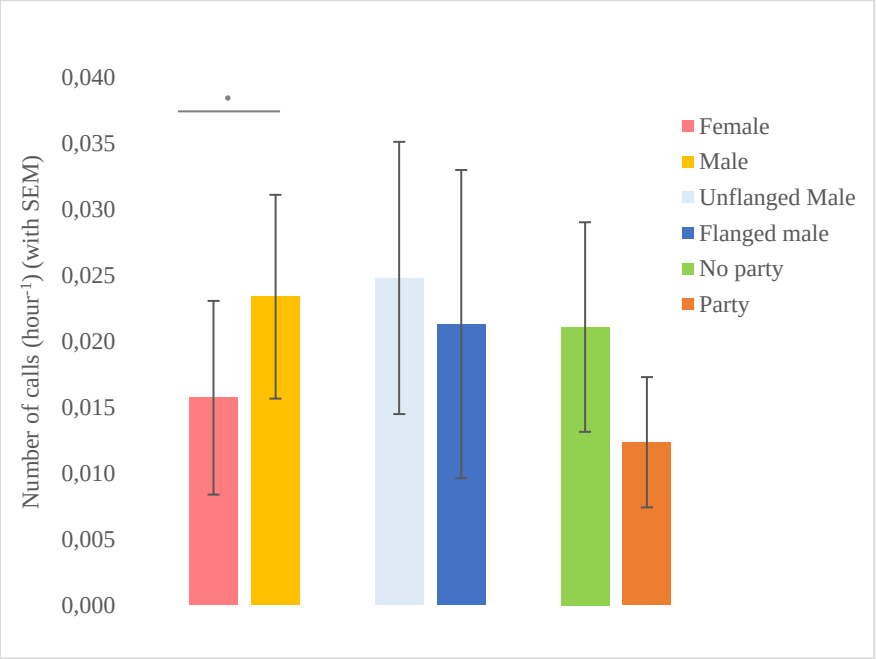

Fig. 3.10 - Mean alarm call syllable-combinations per hour by Gender, Male-age class and Party, with standard error of the mean (SEM). •p < 0.05.

3.5. Is there a decrease in alarm call rate due to habituation to the human presence?

This analysis is based upon the 10 periods of focal sampling where a focal individual was followed for five consecutive sampling sessions (Table 3.6). The mean difference between orangutans followed for more than one day during a maximum of five consecutive days was 57 days (maximum: 114 days; minimum: 27 days; standard-deviation: 31.6038 days). Upon conducting the comparisons between the five consecutive sampling sessions, significant differences were found, meaning that we can reject the null hypothesis, which states that all sampling sessions have similar call rates. Conversely, there is strong evidence that alarm call rate diminishes significantly as the number of sampling sessions increases: Page's L Trend test: *L* = 2109.598, Z = 19.9940 *k* = 5, *n* = 10, *P*-value < 0.0001 (Figure 3.11).

Table 3.6 - Summary statistics of the mean alarm call rate per hour and sampling session (SS), for each individual followed in consecutive days.

SS	Bendot1	Suci1	Suci2	Irma1	Irma2	Irma3	Madalena1	Ompung1	Ompung2	Brutus1	Mean
1	1.2	0	0	48.6221	9.5669	4.4210	0	39.7109	6.4941	3.7974	11.1211
2	3.7719	0.0778	0	25.49075	18.4472	1.6240	0.0840	9.4901	8.7619	18.5306	8.6648
3	1.3298	0.0795	0	71.1917	5.5555	6.7560	0	2.3695	4.4117	0.5898	9.1801
4	1.8099	0	0	2.3430	0.2702	0.4934	1.7840	0.3524	0.7667	0.5255	0.7995
5	0.0859	0	0	3.7309	0	7.8655	0	1.3392	1.3145	0	1.4336

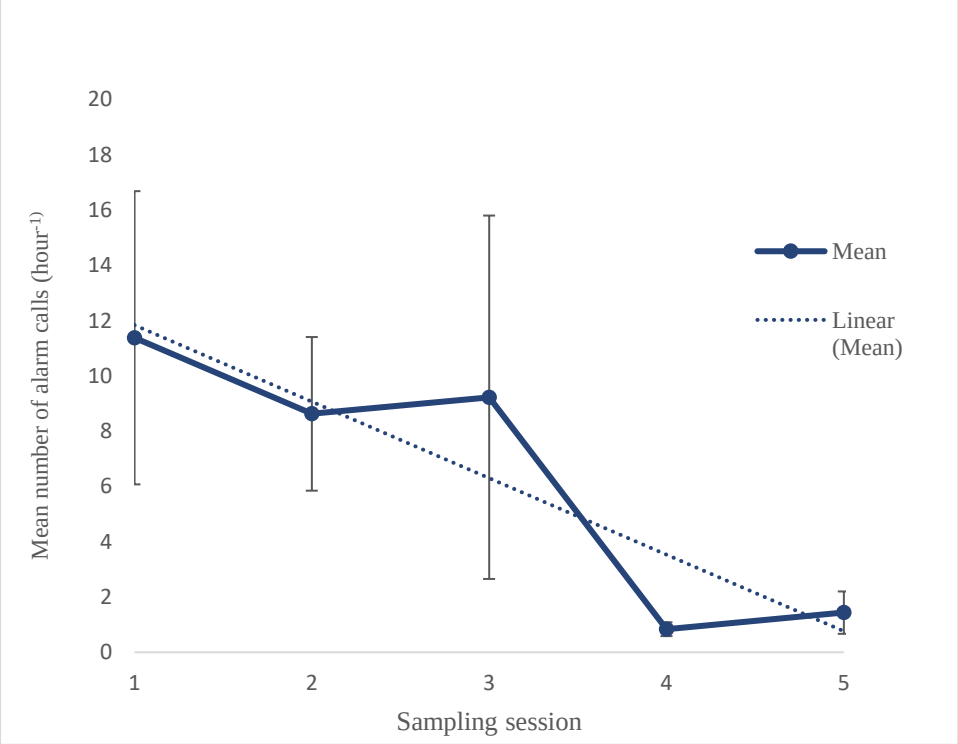

Fig. 3.11 - Mean number of alarm calls towards the observers throughout consecutive sampling sessions, with standard error of the mean (SEM). Linear (Mean) represents mean's linear trend.

3.6. Does alarm call effort towards humans differ from orangutans' alarm call effort towards tigers?

These analyses compare Sikundur orangutans' alarm call effort towards the human observers with reference data from orangutans' alarm call effort towards tigers, considering tiger density at Sumatra. The median call frequency of Sikundur orangutans per sampling session towards the human observers was 0.036 calls per minute (the mean was 0.149 calls per minute), while towards tigers the literature (Lameira et al. 2013a) estimates a higher median frequency of 0.216 calls per minute (Table 3.7). The difference is statistically significant (Wilcoxon one-sample test): V = 0, *P*-value < 0.0001.

For "Alarm call duration", the median towards humans was 8.648 seconds of calling effort per sampling session (or a mean of 36.141 seconds), while towards tigers is estimated to be 20.88 seconds

(Lameira et al., 2013a, Table 3.7), the difference not being statistically significant (Wilcoxon one-sample test): V = 1486, *P*-value = 0.2441.

For "Alarm call state duration", the median towards humans was 157 seconds in an alarm state per sampling session (or a mean of 342 seconds), while towards tigers is estimated to be a smaller duration time of 62.64 seconds (Table 3.7). The difference is statistically significant (Wilcoxon one-sample test): V = 1884, *P*-value < 0.0001.

Considering the comparison with only female data during the first ten minutes of their alarm call response or the first call state, we found that call frequency towards the human observers (median = 0.60; mean = 1.88 calls per minute) was significantly larger than the call frequency towards tigers (Wilcoxon one-sample test: V = 89, *P*-value = 0.024); the call duration towards humans (median = 2.883; mean = 9.174 seconds of calling) was significantly smaller than towards tigers (Wilcoxon one-sample test: V = 16, *P*-value = 0.024); and the call state duration towards humans (median = 69.50; mean = 122.17 seconds in an alarm state) was not statistically different from that towards tigers (Wilcoxon one-sample test: V = 48, *P*-value = 0.505).

Table 3.7 – Summary of alarm call effort for all data and for females only. Q1 = First Quartile, Q3 = Third Quartile. *P*-value comparison with tiger model results. •p < 0.05; *p < 0.01; **p < 0.001; ***p < 0.0001.

	N	**Q1**	**Median**	**Q3**	**Mean**	***P*-value**
All population						
Call frequency	127	0.011	0.036	0.126	0.149	< 0.0001 ***
Call duration	127	3.123	8.648	32.910	36.141	0.2441
Call state	127	58	157	528	342	< 0.0001 ***
Only females						
Call frequency	28	0.200	0.600	2.300	1.880	0.024 •
Call duration	28	0.961	2.883	11.050	9.174	0.024 •
Call state	28	35.250	69.500	126.750	122.170	0.505

4. Discussion

4.1. Synthesis of the results

During the six-month field campaign following wild orangutans at the Sikundur field Station – Gunung Leuser National Park, Indonesia – we recorded vocalizations emitted towards the human observers by ten individuals from all Age-sex classes: four unflanged males, two flanged males, four females and three infants. Our aim was to address the effect of human disturbance stimuli on orangutans, namely how it influences orangutan alarm call behaviour. According to the risk-disturbance hypothesis (Frid & Dill 2002), when human disturbance stimuli are as severe as predator disturbance, it can cause similar risk avoidance behaviours. When such stimuli are particularly invasive and/or chronic, they can divert animals from other fitness enhancing activities, such as feeding, parental care or mating, therefore representing a decrease in wellbeing, survival and reproduction. With this study we aimed to determine whether human presence represents such a disturbance stimuli to the Sumatran orangutan and, if yes, speculate about the consequences of this to the species conservation status.

As our focus were calls directed towards humans, calls from infants were removed from the analysis as they did not interact with the observers, leading to the compilation of an extensive data set: 127 sampling sessions – with a mean of 10 hours and 33 minutes per sampling session – and a total of 1258 hours and 40 minutes of recording. During this period, 6260 calls from all ten adult orangutans were produced towards the observers, subdivided into 13 call categories. Five of these categories were alarm calls, representing 95% of Sikundur orangutans' call effort. From the analysis of these data, we found compelling evidence that the human presence is acknowledged by orangutans; that most of the calls directed towards humans are alarm calls, though there can be some habituation; that the call type most frequently produced is not a vigorous intimidation display, suggesting that orangutans perceive humans as not especially dangerous but, because the human presence is persistent, the effort putt on calling can be similar, and sometimes even higher, than that employed towards orangutans' natural predators. All this together suggest that human disturbance stimuli is not negligible, and that it is probably capable of inducing chronic risk disturbance behaviours, which could be significantly affecting orangutans' wellbeing, survival and reproduction. In the next sections we will thoroughly interpret and discuss each of these results.

4.2. Interpretation and discussion

4.2.1. Orangutan vocalizations towards humans

The first analysis was to determine whether Sikundur orangutans were especially alert to the human presence or if they ignored it most of the time. We found that orangutans are well aware of the human presence, vocalising towards the human observers in most sampling sessions. This demonstrates that humans represent, at least, an environmental stimulus to which orangutans are attentive and responsive.

When analysing the effect of the factors which induce behavioural variability – Gender, Male-age class and presence of Parties – on call presence, some differences were observed: call presence differed between genders, as males had proportionally more sampling sessions with calls than females;

flanged males called proportionally the same number of sampling sessions than unflanged males; and, calls were proportionally more frequent when orangutans moved alone than when in parties. Additionally, females produced as much sampling sessions with and without calls, and the same was found when orangutans formed parties.

Females defend smaller and more stable territories (Rodman, 1973; Rijksen 1978). Consequently, they are regularly within the Sikundur research area and have more contact with the SOCP-YEL staff that monitors the population. Probably because of this, females did not specifically respond to observers, suggesting that they might be more habituated and, hence, less sensitive to human stimuli than males. We have more evidence of habituation in our data, which we discuss in section 4.4, below. Nonetheless, this result can also, or alternatively, be due to the fact that, as most females carried offspring (three out of four, though the forth was pregnant and gave birth later, during the field work campaign), they might have opted to sometimes behave more conspicuously, by producing vocalizations and teaching their children about danger and how to react to it; and other times less conspicuously, preferring to not attract the presence of a predator, a flanged male or simply us. In fact, it were the three parous females that contributed with most call presences from female orangutans, while Madalena, the pregnant orangutan, was rarely observed calling in our presence. This orangutan, however, was also the most studied before our arrival, as she stayed near the research camp site for long periods of time. Madalena low call rates could therefore be due to habituation towards the human observers, or because she did not want to attract any attention due to her pregnancy, assuring a safer condition for her and her progeny. Studying female call rate before and after pregnancy would help to shed more light on this issue.

Males communicate their distress in a more vigorous form than females, using fast movements, branch throwing or menacing displays, such as showing their teeth, while using, or not, vocal signals at the same time. Their bigger overall size compared with that of females may contribute to this behaviour, sometimes trusting only on their visual displays over calling per se. Despite this, males called proportionally more often than females during the sampling sessions, and no differences were observed between unflanged and flanged males. This suggests that size and hierarchical differences between males – flanged males are larger and are dominant over unflanged males – do not affect alarm call behaviour towards humans.

When orangutan individuals met at separate occasions forming sub-groups – i.e. Parties – they called less towards the human observers than when moving alone. There can be at least two different reasons to why this happened: a) orangutan feel safer in groups, as many animals do, due to dilution effects and group defence (Davis et al. 2012), thus lowering their call rate; and b) many times, when in party, orangutans climb considerably higher on trees, thus reducing the predatory or human disturbance risk. The number of individuals within parties was not analysed as most parties were composed of two adult individuals – only once there was a party with three adults – thus lacking data for such a comparison. Larger data sets with different number of individuals would help to study whether larger parties are consistently less vocal towards humans than smaller ones.

4.2.2. Call variability

When addressing whether most calls towards the human observers were alarm calls, 13 call categories (12 distinct call types and one category named “Any”, which was related to calls that we were unable to correctly classify during field work) were found to be used by the Sikundur orangutan population in response to the disturbance stimuli caused by our presence. Out of all calls, alarm calls –

which comprised five of the 12 categories – were found to have higher call rates than the non-alarm call categories. The most frequent call type was, as expected, the Kiss-Squeak, which is orangutans' main vocal response to disturbance (Mackinnon 1971). Kiss-Squeak, which corresponds to 5940 out of the 6260 calls registered during the campaign, was clearly the call with highest rate: 5.6425 calls per hour. Kiss-squeak hand, a variation of the classic Kiss-Squeak, and Grumphs – both alarm calls – were the next calls with higher rates, although much lesser than Kiss-Squeaks': 0.1153 and 0.0381 calls per hour, respectively. The Complex Call presented a call rate lower than the other alarm calls (0.0125 calls per hour), suggesting that such a vigorous intimidation display (Hardus et al. 2009) is not perceived by the orangutans as a useful tool to use towards humans, at least as frequently as the other alarm calls. When testing if alarm call rate differed from non-alarm ones, a significant difference was found, meaning that alarm calls were prominent over non-alarm calls. However, as the sample of Kiss-Squeaks clearly suppressed the others, when removing the Kiss-Squeaks from the analysis no difference between alarm and non-alarm calls was found.

Alarm calls were by far orangutans' first choice to signal the human presence, representing around 95% of all calls and denoting much higher call rates. Nonetheless, it is interesting to note that other non-alarm calls were also used in the same context. These non-alarm calls seem to have an apparent threatening or display use by this species, as we expected from the literature (Hardus et al. 2009a): e.g., Chompings and Grumbles, classic pre-fighting calls between orangutans could be used by orangutans to try a more ruthless/effective way of getting rid of our presence. Another interesting finding was that Chompings, a classic male call, was also observed to be emitted by females in our population, more specifically by Irma and Yanti. The use of long-calls and fast-long calls, essential display and territorial calls, can also be easily comprehended as most are accompanied by a vigorous display that includes breaking trees and charging towards the observers thus menacing any threat towards them. We were lucky enough to see these fast-long calls as they are most of the times performed by transitioning unflanged males into flanged ones, as we observed with Bendot with an early cheek-pad development. The use of these vigorous non-alarm pre-fighting calls in the presence of humans could suggest that orangutans may also perceive humans as direct competitors.

One non-alarm call – Throatscrape – was the most curious finding of all, as this call was supposedly not present in the island of Sumatra but only in Borneo. Additionally, this call was recorded as towards the observers, which is odd as this call is typically emitted in mother-offspring context or when an orangutan expresses submission towards another higher ranking one. Although the use of this call, in similar contexts to this population, cannot be excluded for now, further recordings of these calls on Sikundur could help to better understand their use and context. A similar thing happened with the call Grunt, which is typically used for communication between the mother and her progeny, although we found it also to be emitted towards us, however in a very small frequency. Further recordings of this call are also needed in order to understand its true function on this population and whether it really prevails in contexts such as the one of this work. Rolling call, a call that has been observed to be emitted in combination with Kiss-Squeaks in other camp sites was observed in a low frequency here. Given the fact that this call is not typically considered an alarm-call per se, it still makes sense that orangutans use these calls in such a context of disturbance.

The five calls here considered as alarm calls are typically orangutans' ways of responding to a predator, although Kiss-Squeak was clearly their first response to human disturbance, as seen and described before for all other orangutan populations. Kiss-Squeak Hand, a variation of Kiss-Squeak, was the second most abundant call. We expected that Complex Calls would be more frequent if orangutans perceived our presence as very dangerous. We, indeed, observed a strong response by the orangutans to our presence in terms of body language, but very few vigorous alarm call recordings were made. It seems that orangutans at Sikundur prefer to use more "simple" and less "cost efficient"

vocalizations, such as Kiss-Squeaks, though they could still spend energy with branch throwing or menacing displays.

Previous studies document the fact that infants have been observed to produce "proto-alarm calls" similar to Kiss-Squeaks, indicating that they learn the Kiss-Squeak call at early developmental stages (Mackinnon, 1971). However, in Sikundur, no infant was observed trying to produce any call such as this towards us, reason why infants' calls were not addressed in this thesis. Regarding females, some parous ones – Irma and Yanti – contributed with a large amount of alarm calls for the total data set. The other parous female named Suci, which was the mother of Siboy, called much less than the other two but more than Madalena. Madalena, the orangutan most monitored previous to this study, called very infrequently. However, when she did, she was the first to emit some distinct and sometimes unique calls such as Complex Calls, one of the typical and at the same time most intricate and longer alarm calls in orangutans. This could mean that she put a lot of effort when calling, preferring "quality over quantity". Doubts about the age of this orangutan were often motif of conversation, as some staff members argued that Madalena was older than other female orangutans in the population while others thought that Madalena was younger than most. Either way Madalena, when in party with another orangutan, was always the submissive one, as she did very little calling and tried sometimes to flee from the harassment of not only other females but also from Siboy and Irvan, the offspring of Suci and Irma respectively.

4.2.3. Syllable and combination alarm calls

Focusing now on orangutans' alarm calls only – Kiss-Squeak, Kiss-Squeak Hand, Grumph, Gorkum and Complex Call – we subsequently tested if there was a specific alarm call more frequently used to signal the observers presence. For this, we analysed the alarm calls as syllables and syllable combinations. First, the syllable analysis.

Most of the calls registered were alarm call single syllables – 6153 out of 6260. This makes sense, as these are orangutans' primary responses to danger (Lameira et al. 2013a). It means that orangutans choose most of the times to emit single calls in sequences that can last up to several minutes straight, against combining different syllables into more intricate calls.

Kiss-Squeak and Kiss-Squeak Hand were the most common calls although the first was much more frequent than any other, as shown in the previous section (alarm calls versus non-alarm calls; section 4.2.). The Kiss-squeak has been well mentioned in the literature (e.g. Lameira et al. 2012; Wich et al. 2012; de Boer et al. 2015), as it is the main alarm call produced by orangutans in any population. Kiss-Squeak Hand was mostly observed in sequences of simple Kiss-squeaks. The use of the hand, as described in previous articles (Hardus et al. 2009b; de Boer et al. 2015; Lameira et al. 2013b), serves the orangutan in a way that the lower frequencies produced by this call, comparing to its simple version, helps to deceive the listeners into thinking that a larger animal emitted that call, thus increasing its likelihood to avoid or drive off any potential predator. The Kiss-Squeak with leaves, which is another variation of the Kiss-Squeak with seemingly the same function as the Kiss-Squeak Hand (de Boer et al. 2015), has been observed in other populations (Lameira et al. 2013a) but not in Sikundur, which could support the idea of culture in orangutan calls, as some calls are present in a number of campsites and others are not (Hardus et al. 2009a). Both males and females were observed to emit these calls.

Grumph, the next most common alarm call syllable, was also emitted by both genders although most of these were emitted in combination with Kiss-Squeaks as it was rarely observed to be emitted

alone. The same happens with Gorkum as it was rarely observed to be emitted alone. However, only two females of our population were observed to emit this call – Irma and Yanti – and no male was recorded to do such a call. Previously to our campaign, we expected to observe and record more of these calls, as the literature suggests that these are fairly common amongst different populations, either in Sumatra or Borneo (Hardus et al. 2009a). This did not happened, as perhaps this population relies greatly on the output of Kiss-Squeaks to deter possible danger. In order to understand whether our lack of data on these two calls is indeed a cultural trait of the Sikundur population, more field work would be required.

Complex calls frequency was low, as shown in the previous section (section 4.2), as well. It was only seen to be emitted by the pregnant orangutan, Madalena. The name of this call is very appropriate to its structure and form as it is possibly one of the most fascinating and intricate ones to observe and document (Hardus et al., 2009a). It is a vigorous intimidation display (Hardus et al. 2009) and if humans were perceived as especially dangerous to the orangutans, this call should have been produced very frequently. This was why we expected a higher call rate for this vocalization. Our records for Complex calls towards the observers were from mid-February onwards, however Madalena was observed to emit the same call little time before giving birth towards an animal that was present, possibly a snake or some tree dwelling mammal. It is curious to see that this call was only recorded from an orangutan who was close to give birth, while the literature suggests that this call can be given by both males and females (Hardus et al., 2009a). Whether this is another cultural trait of the Sikundur population, or the literature does not translate the function of this call, we do not know. Further studies are definitely needed.

Comparing with the first analysis (section 4.1.), it is curious that although females vocalise less than males, when they do, they produce more alarm calls than males. This suggests that females tend to perceive humans as predators more often than males, and that they use two strategies to keep safe: either remaining cryptic (silent) or signalling to the human observers that they have been seen (alarm calling). Males, on the other hand, are more responsive to the human presence than females, but seem to perceive humans sometimes as competitors, instead of predators. This is in agreement with the use of territorial pre-fight non-alarm calls by males, as discussed in section 4.2. of the results. Also, as in the first analysis, the behaviour of flanged and unflanged males did not differ, suggesting that behavioural responses to the human presence are not affected by male social dominance. Party analysis showed also a similar pattern with the first analysis, with a lower syllable alarm call rate when in party than when moving alone.

Regarding alarm call syllable-combinations – composed of only alarm call syllables separated by less than one second – they were not as common as syllables alone, as only 106 combination calls were recorded – 105 two syllable alarm calls (Kiss-Squeak + Kiss-Squeak, Kiss-Squeak + Grumph, Kiss-Squeak + Gorkum and Kiss-Squeak Hand + Kiss-Squeak Hand) and one three-syllable combination (Kiss-Squeak + Kiss-Squeak + Kiss-Squeak). The analysis showed relevant overall differences within Alarm call syllable combinations, though post-hoc tests showed no true differences between pairs of combinations. The most common of these combinations was Kiss-Squeak + Grumph, with 38 out of 106, resulting in a mean call rate of 0.0335 calls per hour. Gender, Male-age class and Party analyses showed that males called significantly more alarm call combination syllables than females, that flanged and unflanged males did not differ between them, and that orangutans called similar alarm call combination frequencies when in parties and when alone.

The low rate of syllable-combinations calls can lead to believe that the Sikundur population does not combine calls as much as others do (anecdotal obs.). Nonetheless, Sikundur's orangutans only combined alarm call syllables, thus being safe to assume that call combination's behaviour is associated with alarm calling. Four out of the five alarm calls were found to be combined, with the exception of

the Complex Call. However, orangutans are capable of combining Kiss-Squeaks and Complex Calls, as we observed Madalena do towards an animal threat. Interestingly all combinations were initiated by a Kiss-Squeak, which could lead to believe that the combinations of calls serve as an extension of the Kiss-Squeak's purpose, to deter the danger and manifest the individual's presence. The presence of a three-syllable combination, although interesting, does seem to be rare. Additional field work would allow to gather more data and understand whether this combination in indeed rare, or if it is context in which it applies that is rare.

When looking at the differences between genders, we observe that the pattern changes when compared with single syllables. Here, we witness females having lower call rates than males, and unflanged males with a slightly higher call rate than flanged males. The fact that females combine calls less could be because these calls carry a higher energy output than single syllable calls as they have to care not only for themselves but for their offspring as well. Further studies would be needed to understand whether this can be verified. Males, on the other hand, are larger than females and do not have to take care of the offspring, so call combinations may be less energy demanding and less risky for them. As unflanged orangutans are typically smaller and weaker than flanged males their greater use of these combinations may be to try and compensate for their display upon danger such as human presence. For the parties, orangutans called similar alarm call combination frequencies when in parties as when alone, which is also different from the single syllable results. As call combinations are rare amongst our data we would need a larger data set of alarm call combinations and of orangutans in parties to help better understand these patterns.

4.2.4. Alarm call rate and habituation

When testing whether alarm call rate decayed during follows, we used 10 independent periods from the pool of sampling sessions where focal individuals were followed for five consecutive days. The intervals of time between those periods were also analysed, resulting on an average of 57 days. Results allowed to reject the null hypothesis that consecutive sampling sessions have similar call rates. On the contrary, we found that call rate diminishes as the number of sampling sessions increases, thus providing evidence of habituation towards the human observers.

This decay in call rate throughout time, was expected as the presence of humans in orangutans' natural habitat is frequent and often invasive. Therefore, Sikundur's orangutans should have easily become habituated to our presence, thus diminishing their call rate and begin acting in a more natural and harm-free way. Our expectations met the results, as these showed that effectively their call rate had a decay throughout time. One very good example of this is the behaviour by Irma, one of the orangutans with the highest calling rate of all members of the population, changing from around 70 calls per hour on the third period of five days to not more than four calls per hour on the fifth period of five days.

Some of these orangutans, including Irma, were followed for more than five days in a row, reaching a maximum of 10 days. However, as the test we used (and that we thought to be the most correct one to apply here) did not comply with missing values, only periods of five days (or less) were considered because were common to all focal individuals.

It is interesting that in the first three days of monitoring no call rate decay was observed only after decreasing significantly. This could indicate that orangutans need a period of, at least, three days to gain confidence with the same group of humans, assuming that it does not represent a threat (as it was our case). Curiously, the third day had even a higher call rate than the second. This could still represent orangutans' behavioural pattern before habituation, or be simply circumstantial, that is, an effect of the

animals' dispositions, or a day where they crossed areas where they felt more vulnerable. Perhaps more data from more orangutans over longer consecutive periods of time would eventually show a monotonically decreasing pattern of call rate decay.

Even though an overall pattern of habituation seems clear, most orangutans continued calling across time, which is also a good sign, as they should always keep their guard for humans or any other menacing force that could have implications to their survival. Also, orangutans that called very frequently in the first days continued to call more frequently than the others throughout consecutive sampling. Differences in age, status in the population and personality may help to explain such differences. In the same way as in humans, their personalities and life histories may determine their exposure and use of calls to deter danger, rather than trying to escape or remain cryptic in the canopy.

Our results also suggest that, if we are to record and better understand orangutan's natural behaviour – apart from alarm calling, but more towards ecological traits such as foraging or any other fitness related activity – we should remove at least the first three days of follow from the database, as these are surely biased towards the orangutans' intent to remove the observers from the area. Unfortunately this can also work against the conservation of these animals, as a higher degree of habituation could also leave room for poachers or any other human with lesser good intents that could take advantage of such a fact.

When we followed these orangutans, although our team consisted of around six people taking turns following these individuals, when an orangutan woke up, the survey team could be composed differently from the day before. However it is safe to assume that they recognize at least some of the researchers thus possibly using that information for their benefit and act less stressed. However, this would be very interesting to test: understand whether the people following them has any influence on their behaviour and thus understand whether they would act according to the human individual or independently of this fact, thus generalizing the human observer as a threat or not, across time. We did not tested this hypothesis due to the small sample sizes – as most were carried out by the same two observers – however, with more data and fieldwork this could become a relevant topic when studying orangutan's individual behaviour in the wild.

Our results from this chapter suggest that orangutans – as we would expect from a great ape's ability to remember vast amount of information as potentially our own figurine and face – get more habituated to our presence as time carries on, thus not considering us as such a big threat as they did when we started following them. This is in accordance with the observations made by J. McKinnon in 1974, where he also observed that after three days of following the same orangutans, his presence became almost irrelevant to them. The risk-disturbance hypothesis states that habituation to nonlethal disturbance stimuli can occur, but is generally small or negligible and that, at times, this increased exposure can even lead to increases in animal response. We did not observe a negligible habituation pattern, but not also total habituation. Moreover, as we discuss in the next chapter, we have additional reasons to not dismiss the risk-disturbance hypothesis yet.

4.2.5. Orangutan call effort

Finally, we compared orangutan's population call effort under human disturbance with their call effort under predation risk (Lameira et al. 2013a) at three different degrees: call frequency, where call rate was higher towards tiger models; alarm call duration, where no difference was found; and alarm call state, where orangutans spent significantly more time calling upon human disturbance than when faced with a predator model. To be able to compare our data to a finer degree with that of A. Lameira

and his colleagues (2013a), and to grasp whether there were differences with the predator model we selected only females and their first 10 minutes of exposure to our presence from every period of survey: call frequency was significantly greater for human observers than for the tiger model; alarm call duration was significantly greater for the tiger model than the human observer; and for alarm call state no difference between human disturbance stimuli and the tiger model was found.

A. Lameira and colleagues (2013a) data were collected at Ketambe, another field station also located in North Sumatra, like Sikundur. Tigers are present in both Ketambe and Sikundur, as shown by camera trapping recordings made during the campaign. This, therefore, allowed to understand whether orangutans deviated a considerable amount of time/effort towards our presence when compared with the risk of being predated by a tiger.

Upon comparing our entire data set with the results from the tiger experiment, we observed that call frequency was clearly higher towards tigers than to human observers. This was expected as orangutans should have a more pungent and vigorous response towards their natural predator, that always represent a lethal threat, and with which they have evolved side by side for millions of years (Rijksen 1978). Orangutans and humans also share a common history of thousands of years (Rijksen 1978); however, human disturbance stimuli has radically changed since 1960 (Rijksen 1978), but we do not know whether orangutans are able to adapt or not. Concordantly, when looking at the alarm call duration, orangutans' response towards humans was not significantly different from their response towards tigers. This means that for the duration of alarm calling behaviours, and taking into account the abundance of tigers in Sumatra, orangutans are proportionally perceiving humans as a similar threat to tigers. As for the alarm call state duration, there appeared to be a noteworthy difference between each other and a pattern inversion, as the results show that orangutans spent more time, on average, in a state of alarm towards human observers than tigers. This and the previous result give support to the risk-disturbance hypothesis as human pressure seems to be homologous or even greater than that done by the predation risk. This can be due to the fact that tigers ambush their prey and thus prefer to maintain their position a secret, while our presence was constant (mimicking the humans pressure in orangutans' natural habitat), thus representing a chronic threat, consequently leading to longer alarm call states. On the other hand, these two last analyses can be criticized as we considered human presence to be constant at all times but not tiger presence. This may, thus, have biased the results towards a greater human impact upon orangutans than their natural predator. However, constant human presence in these analyses can also be seen as simulation of the disturbance potential of human beings in orangutans' habitat, as humans are indeed frequently found in and around Sikundur, in activities such as illegal hunting and animal collecting. Nonetheless, data about human density in and around Sikundur, as well as the effective time spent by the orangutans calling towards the tiger model – which would result in finer data for duration and alarm state – would definitely help to have a better grasp and full understanding of the results of such comparisons, that would allow a better validation of the risk-disturbance hypothesis.

4.2.6. Human-caused disturbance *vs* predation risk

Taking all results together, the message is consistent and quite clear: orangutans are sensitive to the human presence; their responses are mainly alarm responses, and despite some degree of habituation, humans are perceived as a threatening stimulus similar to a predator, therefore representing a form of predation risk to Sikundur orangutans. Animals threatened by such aversive stimuli generally shift habitats (Gill et al. 2001; Frid & Drill 2002). However, orangutans' natural habitat is unique in the world and has been progressively reducing (Singleton et al. 2004). They are, therefore, forced to remain in their disturbed habitats, where the time they invest in non-predator avoidance behaviour might be scarce.

If that is the case, it can compromise their wellbeing, reproduction and survival (Gill et al. 2001; Frid & Drill 2002).

Sikundur research facility is very close to both the border of Taman Nasional Gunung Leuser (TNGL) and the Aceh province, which facilitates the intrusion and contact between orangutans and humans from nearby populations that forage for resources, remove native vegetation for agricultural purposes or even hunt and/or harness species for sale in illegal animal markets on this protected land (pers. obs.). Plus, the fact that this forest had been exploited for timber in recent decades (PanEco 2015) may have promoted the contact between some of these highly conspicuous apes and human beings over time, which can alter their response to human disturbance, either by making orangutans more sensitive to humans or less. Our results suggest that despite some degree of habituation, orangutans do not ignore the human presence and that their alarm responses towards humans can be equivalent or even higher than their responses towards their natural predators.

At the rate biodiversity is being lost, both prey and predator seem to be at the hands of human mercy. As tigers are disappearing today at an alarming rate, we can expect humans to fill their role on the pressure done upon orangutans, not only indirectly through forest conversion, but also directly, by our presence and disturbance.

4.2.7. Study limitations

Besides the present study, no other was published on other orangutan population responses to human disturbance, thus comparisons cannot be made. As such it becomes difficult to better understand, or to contextualize, our results. Even comparisons of orangutan calling behaviour in the absence of human presence is impossible, as no such data exist. Every study implies the presence of human researchers. A grid of microphones scattered through the research area would allow to quantify the behavioural difference between presence and absence of human beings, but such a system would be hard to implement.

Searching and following wild orangutan individuals also proved to be a hard and tiresome task. First, as orangutan density in Sikundur is lower than in other research areas such as Ketambe or Suaq, it proved difficult sometimes to find individuals to follow as several days of straight searching passed with no result. Second, as some orangutans showed a bigger discomfort with our presence than others, following them in areas with steep slopes and dense vegetation at ground level – a characteristic of re-growing tropical forests – proved to be a challenging job. However, we managed to get data from what we believe to be a representative orangutan population, as we found individuals from all age-sex classes and from different generations – even the progeny had different ages, ranging from two years to around 6 years old. Nonetheless, we obtained more sampling sessions of females than males (86 and 41 respectively). This can be due to fact that females are philopatric, remaining for the most part in the research area, and males seem to drift around a larger area looking for mates and resources, being harder to be observed. As we would not follow the same orangutan again within a period of one month, when that period finished, our probability of finding female orangutans was considerably higher than finding orangutan males.

Call description also proved to be a somewhat challenging task, as many reference calls in the literature do not prepare unexperienced observers to go into the wild and deal with the individual variability that occurs within calls. However, we stand by the results presented on this thesis, even though anyone who has ever done such a work in the wild knows how difficult it can be at times to

separate and contextualize calls and behaviours that we try to treat as discrete but for an orangutan could be a continuous non-independent flow of behavioural responses. This, is in fact, one of the most basic difficulties on trying to understand animals' behaviour and/or complexity from our anthropogenic perspective.

Audio-recordings were also difficult to obtain, representing only around 2/3 of the total orangutans' vocalization recordings. This had a special impact on the assessment of orangutans' alarm call state duration. The remaining 1/3 of the recordings relate to periods where, sometimes, orangutans spent most of the day calling towards the observers. Not being able to audio record these moments was due to the fact that we had some problems with one of the microphones during the campaign: our memory cards where of small storage – as some equipment was not so recent – and most batteries had a low chargeable potential which lead to periods where we could not record with our equipment.

Besides the fact that human density and a more precise measurement of orangutan's response to the tiger model in what regards the duration of calls and alarm state would be key, one additional behavioural measure that could have helped to study orangutans call effort towards humans was the recovery time between alarm states. If recovering time is long and if during that time orangutans are still not performing other behaviours besides being alert towards potential human threat, this would mean that human disturbance stimuli can be much more stressing than what our data suggest. An ethogram of orangutans' daily activity would have allowed to obtain this kind of data, however we were not able to get access to it.

Crossing data collected from these techniques with the vocalizations we recovered would definitely help to better comprehend whether or not human disturbance causes serious deviation on orangutan behavioural patterns and if they consequently affect orangutans' time and energy budget and ultimately their fitness.

4.3. Conservation suggestions

Orangutans are, without a doubt, one of the most emblematic species in Asia – as well as in the whole world. They are at the same time one of the species – along with their natural predators, the Sumatran tiger – that needs a larger effort from humans to their conservation. Human population growth in Indonesia and Borneo, the continuous forest removal and land conversion for some products whose demand is extremely high worldwide, such as palm oil, accompanied by hunting and illegal trade posts, are the XXI century threats towards the great reddish ape of Southeast Asia (Corlett 2007; Gaveau et al. 2009; Wich et al. 2011; Davis et al. 2013; Freund et al. 2016).

Most of the issues that directly impact orangutans are often above the ability of scientific researchers to directly handle. The way land deforestation and conversion progresses, as well as the continuous uprising of ways to profit from wildlife, results from the responsibility and sometimes negligence of governments and independent companies that explore these areas. Most biologists and other environmental scientists can only advise and suggest ways to better use the ecosystem services and to better preserve the biodiversity inherent to these systems. As I have unfortunately noticed most of the times, the acceptance, understanding and application of these ideas fall short to other benefits that some of these governments favour instead, such as economic ones, which is a sad but also true fact across the globe.

This work attempted to test a hypothesis which can help develop further our current base framework that predicts human's disturbance on wildlife (Frid & Dill 2002). Understanding the

relationship between predation risk and human disturbance (Gill et al., 2001; Frid & Dill 2002; Beale & Monaghan, 2004) and how both impact wildlife is key to the comprehension of animal behaviour (Lima & Dill, 1990; Williams et al,2006; Gill 2007) and its conservation (Kerley et al. 2002; Beale & Monaghan 2004; Williams et al. 2006; Stankowich 2008). As orangutans have slow life histories, they can have greater difficulties at adapting to the diverse array of human disturbances, not only human presence but all actions that affect them both direct and indirectly. This is why when conducting experiments in the wild it is vital that we follow a methodology that disturbs them the least possible.

The habituation we found here is a double-edged sword: on the one hand it can be positive, as their habituation lets orangutans interact with their environment in a non-apparent disturbed attitude but, on the other hand, it can make them more vulnerable to people with shadier intents, such as poachers.

This means though that only because orangutans show some habituation towards our presence, our efforts to protect them should not weaken, by the contraire. However, there are some guidelines that we should follow more strictly in order to maintain their fair health when monitoring them in the wild. We should minimize at all times the number of observers that are following a focal orangutan and, as shown by the call rate decay throughout several days of continuous follows, if we want to obtain a more realistic approach of the natural behaviour of an orangutan, we should not use data from at least the first three days, as orangutans seem more stressed by our presence, thus not acting as they would if there were no humans in the surroundings. Therefore, in studies such as the present one, where understanding the human disturbance effect on orangutans was the objective, all observations should count. However, when trying to study feeding, mating or other type of behaviours directly related to orangutans' fitness and survival, there should be given a time for orangutans to understand that the observers are not a threat, thus acting in a less biased way and allowing the acquirement of data that could best fit and help conserve these extraordinary animals.

Unfortunately, even though Gunung-Leuser National Park is the oldest and one of the most respected protected parks in Indonesia, people enter the park not only to collect animals to sell on trade markets, but also to remove trees. This is worrying, not only for the orangutan, but for all species that constitute those amazingly rich ecosystems. Although many villages still gather resources from the forests as they did centuries ago, the growth of the population and the better access to previously unexplored parts of the forest puts in jeopardy their own future. As we have seen for our data, human presence affected the orangutans in a similarly way as when they face their main predator, which can have serious implications on the time and energy that they spend on their daily activities and body condition.

It is key that local populations understand that they must take care of the forests that surround them and respect all surrounding wildlife, so these can continue providing the services they need. One way of doing this is interacting and drawing in the local communities, as some ONGs already do, to try and convert skilled people like woodworkers or hunters into conservationists and people who care and protect their land and all life within. There should be classes from a young age in order for them to understand the importance of their forests and how they can interact and prosper from it, together with the forest itself. Governments should also think about expanding protected areas with benefits for those who already live inside these regions, so that they feel like they are part of it and have a role in keeping their resources safe. As it is transversal in many areas, education is fundamental to learn that poaching or taking animals from their homes is not a correct way to make a living. From a young age, local people should understand how important and unique all the nature that surrounds them is, and learn how to act accordingly to their needs, the needs of the orangutans and of all the other species.

Sikundur is a re-growing forest whose structure and biodiversity is still recovering today. Allowing this forest to grow and studying how its wildlife responds to its recovery and to the presence

of humans, becomes a fundamental job when approaching the restauration and conservation of ecosystems and their species. This work and all data here presented aims, above all, to address the theme of human disturbance on this critically endangered animal species. We hope this can serve as a base for future comparative works with other orangutan populations, other species and even with animals in captivity, and that it motivates whoever reads it to imagine and design a world where we can learn to cope with each other and grow side by side, man, orangutans and all surrounding nature.

5. References (following "Conservation Biology" guidelines)

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